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Coral-microbialite reefs in pure carbonate versus mixed carbonate-siliciclastic depositional environments: the example of the Pagny-sur-Meuse section (Upper Jurassic, northeastern France)

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Abstract Middle to Upper Oxfordian reefs of a shallow marine carbonate platform located in northeastern France show important facies changes in conjunction with terrigeneous contents. The Pagny-sur-Meuse section shows coral-microbialite reefs that developed both in pure carbonate limestones and in mixed carbonate-siliciclastic deposits. Phototrophic coral associations dominated in pure carbonate environments, whereas a mixed phototrophic/heterotrophic coral fauna occurred in more siliciclastic settings. Microbialites occur in pure carbonate facies but are more abundant in mixed carbonate-siliciclastic settings. Reefs seem to have lived through periods favourable for intense coral growth that was contemporaneous with a first microbialitic layer and periods more favourable for large microbialitic development (second microbialitic layer). The first microbialitic crust probably developed within the reef body and thus appears to be controlled by autogenic factors. The second generation of microbialites tended to develop over the entire reef surface and was probably mainly controlled by allogenic factors. Variations in terrigeneous input and nutrient content, rather related to climatic conditions than to water depth and accumulation rate, were major factors controlling development of reefs and their taxonomic composition.

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Introduction

In the Late Jurassic, the conditions along the northern margin of the Tethys were favourable for intense reef development (Kiessling et al. 1999; Leinfelder et al. 2002). Among the different reef types recognized in the Upper Jurassic (Leinfelder 1993; Leinfelder et al. 1994), coral-microbialite reefs are abundantly represented in the Oxfordian (Helm and Schülke 1998; Bertling and Insalaco 1998; Dupraz 1999; Dupraz and Strasser 1999, 2002). Some palaeoecological studies have been carried out on coral-microbialite reefs and some palaeoenvironmental models have been proposed on the development of coral and microbialitic crusts (Insalaco et al. 1997; Helm and Schülke 1998; Bertling and Insalaco 1998; Dupraz and Strasser 1999, 2002).

In northeastern France, Middle to Upper Jurassic deposits are rich in coral reefs (Geister and Lathuilière 1991; Lathuilière et al. 2003). The section of Pagny-sur-Meuse exhibits a succession of well-exposed and diverse bioconstructions. In addition, it shows a vertical transition from pure carbonate depositional environments in the Middle Oxfordian to a mixed carbonate-siliciclastic regime in the Upper Oxfordian. According to the depositional setting, bioconstructions reveal a diverse coral composition and a more or less significant development of microbialites. Sedimentological studies made in the Swiss Jura and other regions of the northern shelf margin of the Tethys have equally shown that a probable important climatic change occurred during the Middle to Upper Oxfordian transition (Gygi 1986; Gygi and Persoz 1986; Pittet 1996; Pittet and Strasser 1998; Cecca et al. 2001; Martin-Garin et al. 2002). Despite the excellent quality of the outcrop, only a few studies were made previously on the Pagny-sur-Meuse section, and palaeoecological and sedimentological analyses have only been incompletely carried out (Geister and Lathuilière 1991; Laternser 2000; Vincent 2001; Carpentier et al. 2002a; Lathuilière et al. 2003).

The aim of this paper is to present a palaeoecological study of the different reef systems jointly with a detailed sedimentological analysis of non-constructional lateral deposits, as well as to provide information on the internal reef growth patterns. In addition, we relate the vertical distribution of reef communities and the response of coral-microbialite reef growth to the increase of terrestrial run-off that occurred during the Middle to Upper Oxfordian transition.

Geological framework

Upper Jurassic deposits of the eastern margin of the Paris Basin are accessible in an arc-shaped exposure belt delimited in the north by the Brabant-Ardennes Massif, in the east by the Vosges Massif and in the south by the northern foothills of the Massif Central (Fig. 1A). During the Middle to Upper Oxfordian time, the wider study area was located at the northwestern margin of the Tethys Ocean, between latitudes 20–30°N (Fig. 1C; Dercourt et al. 1985; Ziegler 1990). A merely moderate subsidence rate coupled with high carbonate productivity resulted in a shallowing-upward trend already recognizable in deposits since Lower Oxfordian time. This trend was recorded all over the Paris Basin (Jacquin et al. 1998; Guillocheau et al. 2000). It allowed the development of the shallow carbonate platform of Lorraine in the area between the Ardennes and the Marne Valley (Humbert 1971; Marchand and Menot 1980; Geister and Lathuilière 1991; Collin and Courville 2000).

This platform shows a strongly variable facies from pure carbonate to mixed carbonate-siliciclastic deposits. The important siliciclastic input is usually attributed to the erosion of the Brabant-Ardennes Massif, which is located about 100 km to the north (Ziegler 1990; Cecca et

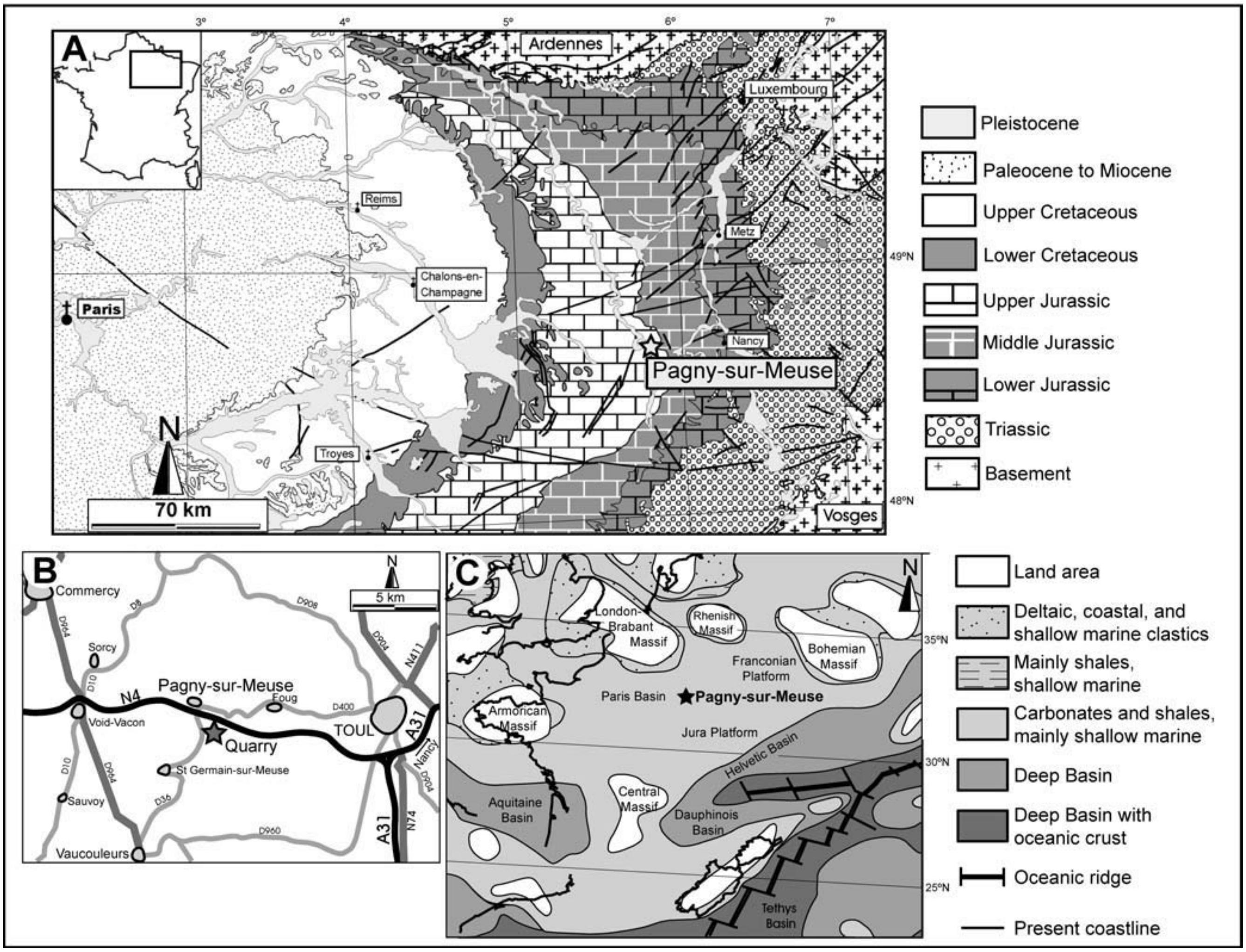


Fig 1 A–B Location maps of the quarry section studied at Pagny-sur-Meuse. **C** Paleogeographical reconstruction of the northern margin of the Ligurian Tethys during Callovo-Oxfordian time based on Dercourt et al. (1985), Ziegler (1990) and Thierry (2000)

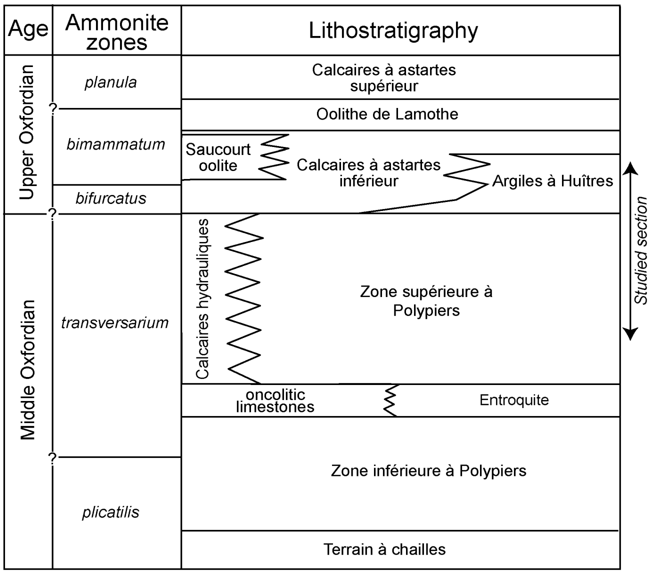


Fig. 2 Stratigraphic framework of the Oxfordian in Lorraine based on Humbert (1971), Marchand and Menot (1980), and Enay and Boullier (1981). Note the uncertainty in the position of the boundaries of the Middle-Upper Oxfordian and *bimammatum - planula* Zones in the Pagny-sur-Meuse section

al. 1993). The Lorraine Platform is limited near the Marne Valley by a shoal area (Carpentier et al. 2002b), previously interpreted as a reef barrier (Humbert 1971; Debrand-Passard et al. 1980; Marchand and Menot 1980). From here, there are lateral transitions into the sponge-bearing deeper shelf deposits of the Jura Mountains and into the marl-limestone deposits with sporadic pseudo-bioherms found in the Dauphinois Basin (Gaillard 1983; Enay et al. 1988; Gaillard et al. 1992).

Outcrops of the Oxfordian reef formations of the eastern Paris Basin are characterised by two successive reef complexes (“Zone inférieure à Polypiers” and “Zone supérieure à Polypiers”; Geister and Lathuilière 1991; Fig. 2). The two reef complexes were also named “zone construite inférieure” and “zone construite supérieure” by Humbert (1971), “Complexe récifal inférieur” and “Complexe récifal supérieur” by Hilly and Haguenauer (1979), and “Episode récifal inférieur” and “Episode récifal supérieur” by Marchand and Menot (1980). Both reef formations are of Middle Oxfordian age. The lower reef formation developed during the upper part of *plicatilis* Zone and the lower part of *transversarium* Zone. The upper reef formation extends further into the *transversarium* Zone (Enay and Boullier 1981). The overlying deposits (“Argiles à Huîtres”; Marchand and Menot 1980) are dated as Upper Oxfordian (*bifurcatus* to *bimammatum* Zones, see Enay and Boullier 1981).

At Pagny-sur-Meuse (located about 33 km W of Nancy) the transition between the Middle and Upper Oxfordian beds is accessible in a huge quarry exploited by the Novacarb Company (Fig. 1B). Due to continuous quarrying, a fresh accessible outcrop face is maintained, which is suitable for detailed study. Three quarry faces perpendicular to each other are oriented N–S, E–W, and S–N. Each of them is well-exposed laterally over approximately 100 m. The total thickness of the series is around 95 m with the most complete section in the southern face of the quarry. In the two remaining faces, the top of the section is not exposed or already eroded.

The rocks at the base of the Pagny section formed during a first major reef-building event. They are overlain by thick, white chalky limestones corresponding to the middle and the upper part of the upper reef complex (Fig. 2; Geister and Lathuilière 1991). These rocks are excavated for the chemical industry because of their high calcium carbonate content (up to 98.8% of $CaCO_3$). The upper part of the section shows a succession of marls and bioclastic limestones that contain minor isolated bioherms

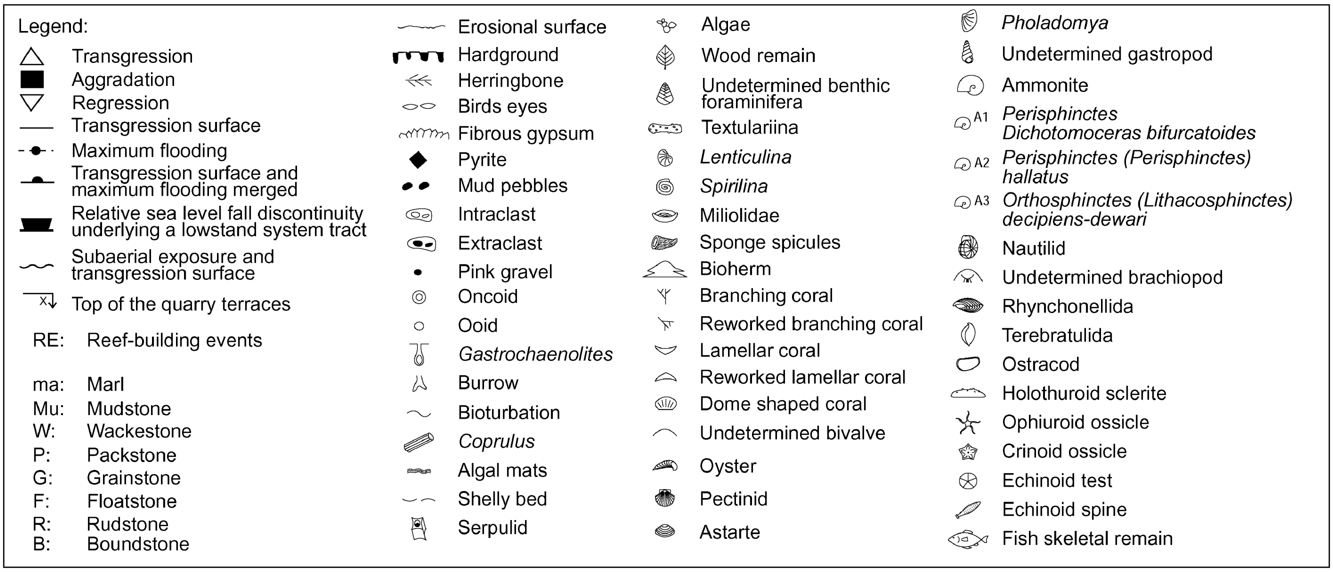


Fig. 3 Legend to Fig. 4

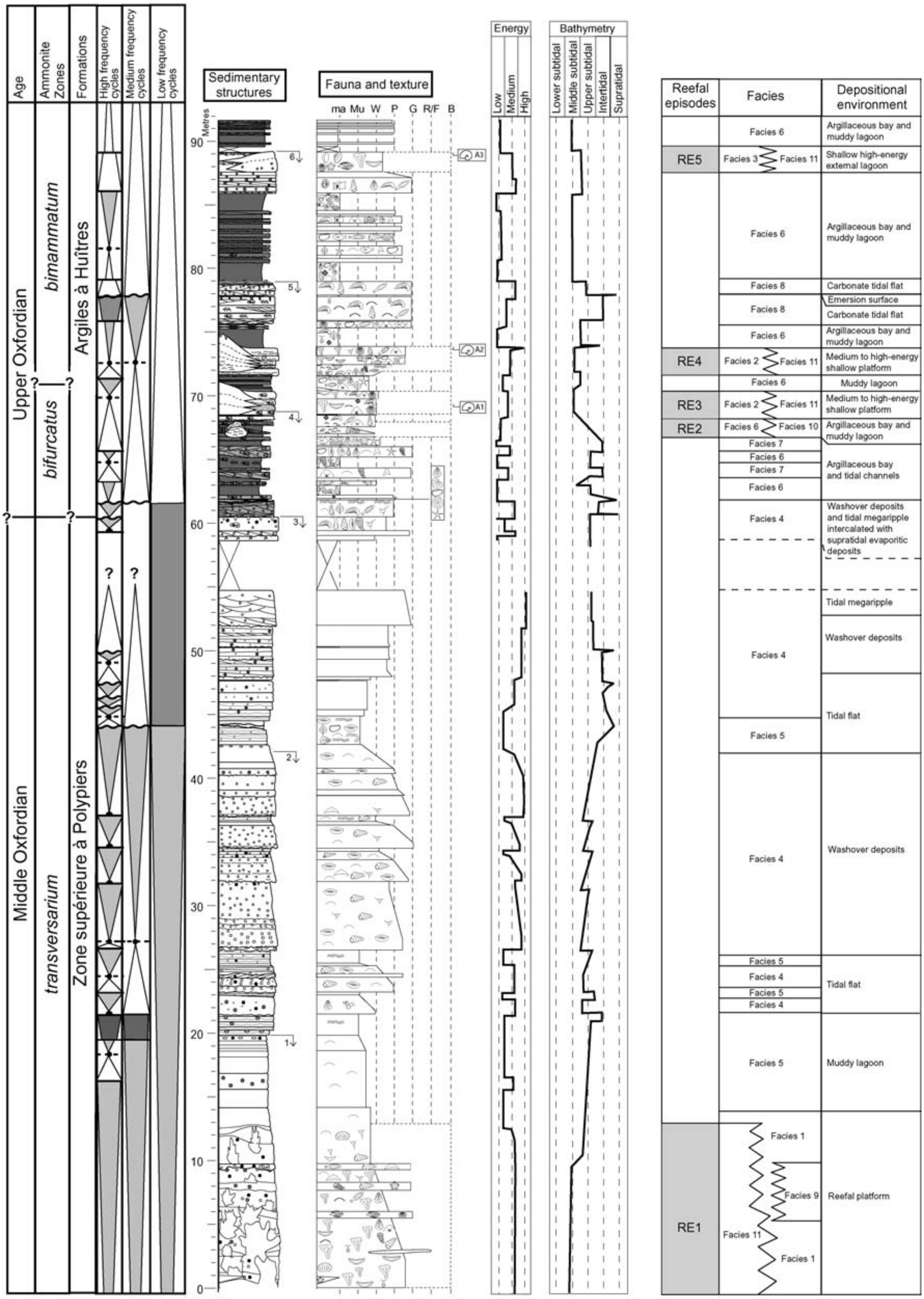


Fig. 4 Description and depositional sequences of the Pagny-sur-Meuse section. For location see Fig. 1. Facies description in Table 1. For legend see Fig. 3

(Maubeuge 1968). The new discovery of the ammonites *Perisphinctes (Dichotomoceras) bifurcatoides* and *Perisphinctes (Perisphinctes) hallatus* (det. R. Enay) allows us to place the limit between the *bifurcatus* and the *bimammatum* Zones somewhere in the 69–74 m interval of the section (Figs. 3 and 4).

Methods

Reef morphology, framework composition and transition into lateral sediments were studied in the field. The stepwise quarrying allowed sedimentological sampling bed-by-bed. For safety reasons, below the high quarry faces, only freshly quarried blocks have been analysed. Relative (surface) proportions of framebuilders were obtained by laying a 1-cm grid on random reef surfaces and point-counting at the intersections. This last method was less convenient in some parts of the reefs due to irregular quarry surfaces. Thus, a line transect method also had to be used. The combination of both methods permitted the estimation of the general proportion of reef components (Dodge et al. 1982; Bernecker et al. 1999). Numerous polished slabs and 160 thin-sections were used to study the facies, microfacies and microbialite microfabrics. The relative abundance of micro-encrusters associated with microbialites was assessed on a scale ranging from 0 to 4 (0 = not observed; 1 = rare; 2 = present; 3 = common; 4 = abundant). The reef fabric and the relationships between the elements of the framework were studied on 60 large, oriented and polished slabs. In addition, 209 coral samples were randomly collected in selected bioconstructions of the successive reef-building events. Transversal and longitudinal coral sections in polished slabs as well as thin-sections were used to identify scleractinian genera.

Sedimentary context

Facies types and depositional environments

The 95-m-high quarry section can be subdivided into a lower segment of pure carbonate facies accessible in the three lower stepped quarry faces and an upper segment of mixed carbonate-siliciclastic deposits represented by bioclastic limestones rich in siliceous material and by marls (Fig. 4). The latter corresponds to the four main quarry walls in the upper part of the quarry. Eleven facies types were recognized and their classification is given in Table 1. Facies types are macro- and microscopically

Table 1 Classification and environmental interpretation of the facies. See Fig. 4 for their stratigraphic position in the Pagny-sur-Meuse section

Facies	Description	Texture Dunham (1962)	Main elements	Other elements	Sedimentary features	Depositional environment	General environmental interpretation
1	Pure carbonate limestone	M->G	Peloids (< 0,2 mm), *Paracidaris,* gastropods	*Solenopora*, calcareous sponges, rhynchonellids, fragments of *Bacinella irregularis*, *Pentacrinus*, bioclasts of branching and massive corals (e.g. *Stylosmilia*)	Ravinement surfaces, crinoidal tempestites	Open lagoon / inter-reefal environment	Moderate-energy carbonate platform (with episodic high-energy events)
2	Bioclastic limestone	W->G	Oysters, echinoderms, agglutinating foraminifera	Gastropods, ostracods, pectinids, serpulids, crinoid ossicles, calcareous algae, bryozoans, ammonites, mudstone extraclasts, pyrite, peloids, and brachiopods	Fining upward shelly layers	Storm dominated	
3	Oncolitic and bioclastic limestone	M-> P	Nubecular oncoids	Sea urchin spines, oysters, brachiopods, crinoidal elements, *Pholadomya*, nautilids (*Paracenoceras*), gastropods, ostracods, pectinids, serpulids, bryozoans, ammonites, and mudstone extraclasts	Graded layers with an horizontal lamination (tempestites)	Shallow and external lagoon	
4	Oolitic and oncolitic limestone	P->G	Ooids and oncoids	Reworked algal mats, nerineid gastropods, miliolids, textularids, bivalves, sparse and isolated corals (e.g. *Stylina*)	Fining upward beds with planar lamination, cross-bedded stratifications, angular oblique stratification	Back-reef shoal, washover and spillover lob deposits	High-energy open lagoon
5	Algal mats an bird eyes	M->W	Algal mats	Bivalves, miliolids, ligneous remains, black pebbles, and ostracods	Bird eyes, tepee structures, amalgamated tidal channels	Tidal flat	Very shallow subtidal to upper intertidal lagoon
6	Marl dominated with calcareous beds	P->G	Oysters, brachiopods, and echinoderms	Quartz grains (10%), framboidal pyrite, glauconite, *Spirillina*, *Lenticulina*, coarse agglutinating foraminifera, *Coprulus*, serpulids, gastropods, fish teeth, ostracods, *Astarte*, bryozoans, holothuroid sclerites, ophiuroid ossicles, siliceous sponges spicules, crinoid ossicles, and wood remains (*Brachyoxylon*)	Coarse shelly tempestites, gradded tempestites (ideal tempestite sequence of Aigner), wave ripples	Argillaceous bay and muddy lagoon (tidal flat + mangroves?)	Low-energy carbonate platform (with episodic high-energy events) open lagoon
7	Oolitic and extraclast limestone	G	Ooids and extraclasts containing sponge spicules	Agglutinating foraminifera, quartz grains, broken bivalves, *Lenticulina*, siliceous sponge spicules, miliolids, and ophiuroid ossicles	Tidal channels with discontinuous clay drapes	Subtidal to intertidal shallow lagoon	Carbonate high-energy (tide dominated) shallow, and proximal platform
8	Oyster shell limestone	G	Oyster shells	Brachiopods, echinoderms, and gastropods	Low angle stratifications, herringbone stratifications, encrusted and bored subaerial surface	Beach to submersive carbonate tidal flat	
9	*Bacinella irregularis* bafflestone	B (bafflestone)	*Bacinella irregularis*	Peloidal leiolite and allomicrite	Alveolar growth form	Algal-cyanobacterial meadow	Reefal environment
10	Oyster reef	B (framestone)	Cemented oysters (*Nanogyra nana, Praexogyra*)	Bryozoans, serpulids, microbialites, and nubeculariids		Oyster reefs	
11	Coral-microbialite reef	B (framestone)	Corals and microbialites	Bivalves, micro-encrusters, and brachiopods		Coral reefs	

defined by their texture, their composition (main and secondary components) and by their sedimentary features. Each facies type is interpreted in terms of a particular sedimentological setting within a wider depositional context at the scale of a carbonate platform (e.g. proximal/distal positions, open/restricted environments, and low/high energy). The respective position of facies types in the section is shown in Fig. 4. Facies types 1–8 correspond to non-framework deposits and facies types 9–11 correspond to boundstones.

Five successive reef-building events (RE1–RE5) are depicted separately (section 5). They include oyster reefs (facies 10; RE2) and coral-microbialite bioherms (facies 11; RE1, RE3–RE5). Locally, *Bacinella* bafflestones (i.e. facies 9) are observed laterally on RE1 reefs. In general, the carbonates were deposited in environments ranging from shallow reef platform (probably about 10 m deep) to supratidal flat. Marly levels correspond to environments ranging from a shallow bay setting (and subemersive tidal flat) to a storm-dominated open lagoon. Remains of vegetation (e.g. *Brachyoxylon*; det. M. Philippe) in the argillaceous environments suggest that land was not far or that mangrove-type biotopes were present (Garcia et al. 1998). On the other hand, comparison with tempestite sequences described by Aigner (1985) suggests that depositional environments may have been 7–15 m deep, which is above fair-weather wave base.

Facies succession and depositional sequences

The segment of the Pagny-sur-Meuse section consisting of pure carbonate (including RE1 reefs) suggests deposition during a low-frequency shallowing trend in its lower part (Fig. 4). In its upper part, despite an increase in siliciclastics, a general low-frequency transgressive phase permitted colonial corals settlement and the development of reefs corresponding to reef building events RE2, RE3, RE4, and RE5.

The lowermost part of the pure carbonate section shows the transition from a coral-microbialite reef (RE1) to a muddy lagoon with algal mats. This indicates a shallowing-up trend that led to more protected and nearly supratidal environmental conditions. More open facies units point to higher energy conditions (washover deposits), which were due to a transgressive pulse resulting in a general backstepping of the depositional environments on the platform. This transgressive period consists of shallowing-up elementary units, which correlate with other sections from Lorraine (e.g. Saint-Germain-sur-Meuse; Carpentier 2004), corresponding to parasequences (Mitchum and van Wagoner 1991). The maximum flooding is characterised by the thickest parasequence with the most distal facies. Subsequent elementary units show more proximal facies with the thinnest washover deposits, illustrating the decrease of the available space. This regressive trend led to growth of intertidal algal mats and formation of amalgamated tidal channels rich in wooden debris. This suggests a regressive maximum at the base of the third quarry face. New washover deposits and subtidal megaripples indicate another phase of retrogradation. A hardground and an erosional surface with supratidal algal mats reveal a new regressive maximum towards the end of the pure carbonate deposition (Fig. 4). These emergences did not result from gradual shallowing-up due to deposition, but rather corresponds to discontinuities, which formed as a result of relative sea level fall. The discontinuities mark a sequence boundary interval (*sensu* Vail et al. 1977), which precedes a phase of abundant terrigeneous input.

The mixed carbonate-siliciclastic segment of the section corresponds to a new phase of inundation accompanied by the deposition of marls exhibiting plurimetric tidal channels and oyster reefs (RE2). These beds are followed by a more open facies with bioclastic limestones and coeval coral-microbialite reefs (RE3). A maximum flooding event probably occurred during the development of RE3 and RE4 reefs, just before the beginning of a rapid regression marked by shallow marls and intertidal oyster shell deposits (exposed at the top of the fifth quarry face). The sequence boundary is indicated by a bored hardground. After this regression, more open facies and higher energy conditions are indicated by the deposition of marls with storm deposits and by oncoidal limestone with coral-microbialite reefs (RE5).

Carbonate vs. mixed carbonate-siliciclastic depositional environments

Sedimentary facies and fossil assemblages both point to very shallow water during all the reef-building events and non-reef intervals. Some influence of the open ocean is suggested by very rare finds of ammonites. The water depth probably did not exceed tens of metres or even a few metres (Fig. 4). Major sea-level fluctuations were observed in the lower half of the section but did not affect carbonate sedimentation in this extensive and flat epicontinental platform (Carpentier 2004). However, such changes can be directly responsible for the opening or closing of a shallow lagoon (Dupraz 1999; Dupraz and Strasser 1999, 2002). This is probably the case for the Upper Oxfordian deposits of northeastern France, where a shallow-water area formed a hydrodynamic barrier near the Marne Valley, which separated a large lagoonal realm in Lorraine from the open sea (Humbert 1971; Marchand and Menot 1980; Carpentier et al. 2002b). An opening towards the northeast is also probable as it is documented for the Middle Oxfordian (Carpentier et al. 2004). Thus, slight depth variations may explain recurrent facies changes between the marl deposits of facies 6 and the bioclastic carbonates of facies 2, 3, and 8. In these mixed carbonate-siliciclastic settings, temporary gaps of the lagoon towards the open sea allowed a higher carbonate production by considerable seaward export of terrigeneous particles, permitting the deposition of more pure bioclastic limestones. On the contrary, during periods of closure, clay input and nutrient levels increased and lowered carbonate production, resulting in marl deposits (Ehrlich 1996; Dupraz and Strasser 2002).

Nevertheless, such a sea-level fluctuation cannot be the only cause for the drastic facies change observed, ranging from pure carbonates to mixed carbonate-siliciclastic deposits. During the Middle–Late Oxfordian transition, a tectonic activity seemed to occur in Lorraine (Carpentier 2004). However, the remarkable rise of terrigeneous input from the hinterland during the Middle to Upper Oxfordian transition was not only triggered by eustasy and/or tectonic uplift but also driven by the increase in terrestrial runoff, which led to variations of the trophic level in these shallow platform environments. Previous large-scale investigations in the shallow lagoon of the Swiss Jura Mountains along the northern Tethys shelf revealed that the main cause was probably the shift from a dry to a more humid climate (Gygi 1986; Pittet 1996; Pittet et al. 1995; Pittet and Strasser 1998; Dupraz 1999; Cecca et al. 2001; Martin-Garin et al. 2002).

Reefs

Reefs are well developed and show great variations in size, shape and composition (Fig. 5A, C, D, E, F). These bioconstructions grew up during five reef-building events, which have been analysed all along the Pagny section. The reefs can be subdivided in two main types: coral-microbialite reefs and oyster reefs. Coral-microbialite reefs are observed both in the limestone-dominated section and in the mixed carbonate-siliciclastic depositional environments, whereas small oyster reefs are confined to marl deposits (Fig. 4).

General reef description

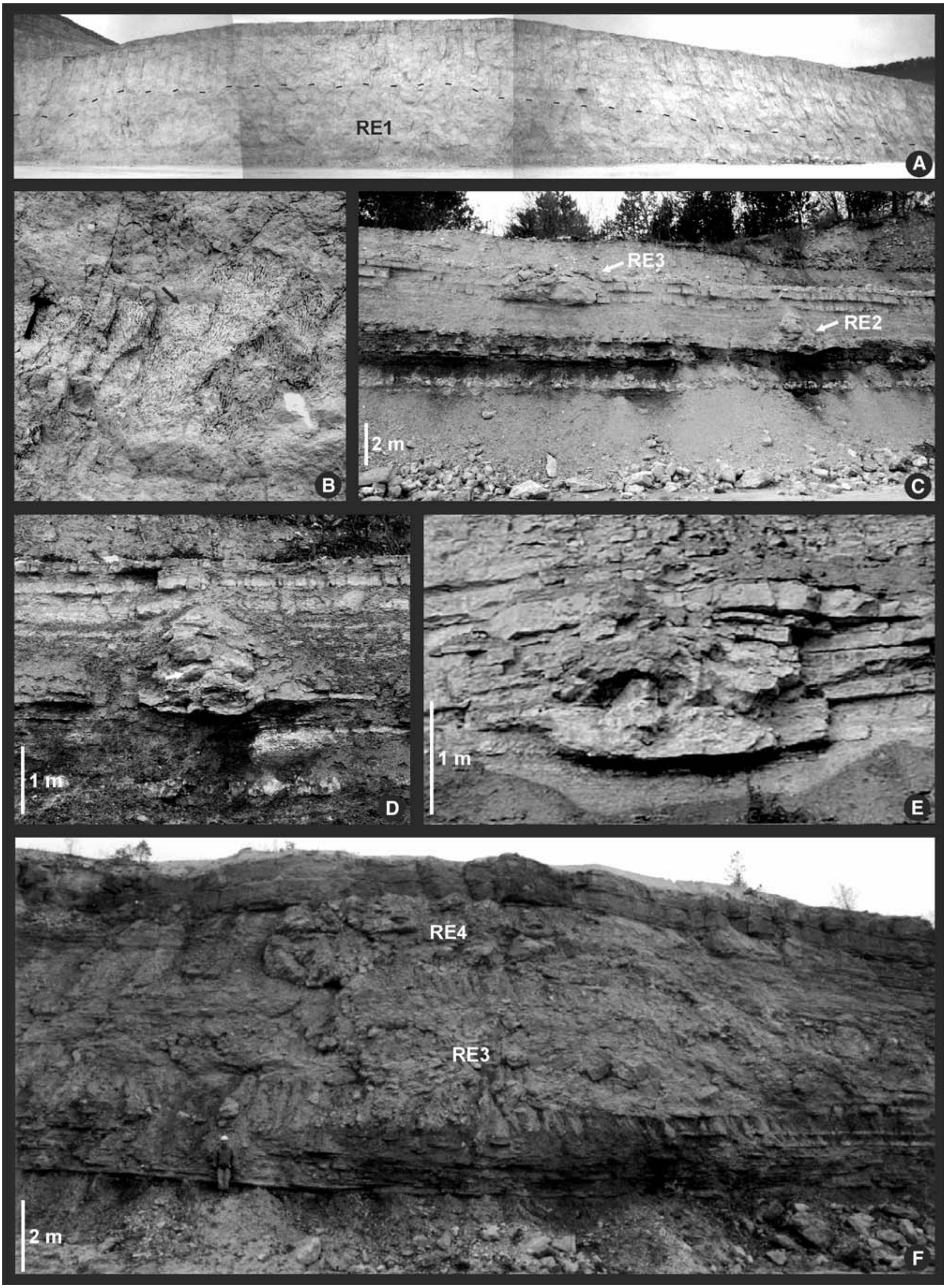
Coral-microbialite reefs

The first reef-building event (RE1 in pure carbonate settings) is represented by reefs of large dimensions (Dagallier et al. 2000) extending across almost the entire width of the section. Laterally, the reefs are in contact with the white limestones of facies 1. Without their base, which is not exposed, the reefs are up to 15 m high and at least 100 m wide having an overall convex upper surface (Fig. 5A). The most abundant metazoans in RE1 reefs are corals (about 61% of the reef volume) dominated by phaceloid genera (*Aplosmilia* and *Stylosmilia*) and massive *Stylina* (Figs. 5B, 6 and 7). An up-to-5-cm-thick crust of microbialites (16%) is frequently observed on this primary framework (Fig. 8A). Other common skeletal components include bivalves (bavekelliids, pteriids, and pectinids), gastropods, brachiopods, echinids, and the red alga *Solenopora*. Bivalves contribute to about 12% of the reef volume. The volume of intra-reef sediments amounts to an estimated 11%. These coral-microbialite reefs show numerous surfaces of growth interruption due to necrosis. Generally, large colonies of *Aplosmilia* are truncated. The truncation plane served as a substratum for new coral settlement and growth (Fig. 5B).

In mixed carbonate-siliciclastic depositional environments, coral-microbialite reefs are common and formed during three successive reef-building events (RE3, RE4, and RE5; Fig. 4). These metric to decametric build-ups have a lenticular shape and show surfaces of reef growth interruptions, which are laterally correlated with contemporaneous non-reef limestones. Reefs of RE3 and RE4 occur laterally on facies 2 (Fig. 5C). RE3 reefs are characterised by both small metric patch-reefs and decametric bioherms, which are ovoid to lenticular in shape (Fig. 5E, F). Coral diversity is lower here than in RE1 reefs, but microbialites appear to be more abundant (approximately 20–30% of the reef volume). The associated fauna consists of numerous oysters, cemented bivalves, brachiopods, and gastropods. RE4 reefs correspond to the plurimetric coral-microbialite bioherms that developed either directly on top of a pre-existing relief created by RE3 reefs (Fig. 5F) or occur laterally. Main reef components are corals (35%), locally with decimetric to metric accretions of cemented bivalves (33% of ?*Eoplicatula*). Microbialites are moderately developed (16%). Centimetric to decimetric oyster crusts (8%) are observed at the underside of some phaceloid colonies. Other faunal components (e.g. echinids and brachiopods) represent 2% and sediments 5% of the reef volume. Laterally on the oncolitic and bioclastic limestones of facies 3, a few metric coral-microbialite patch reefs characterize reef-building event RE5. Microbialites dominate these bioconstructions (56%). Other components are corals (19%) and associated organisms (e.g. oysters and other bivalves, sponges, and echinids; 20%), while intra-reef sediments represent also here only 5% of the total reef volume.

Oyster reefs and frame-building bivalves

RE2 reefs are small oyster bioconstructions intercalated in marly environments of facies 6 just above the tidal channels of facies 7 (Figs. 4 and 5C, D). These patch reefs are about 1–2 m in horizontal diameter with a height not exceeding 1.5 m. Their generally ovoid shape results from the agglomeration of pluridecimetric mammilated accretionary units forming a framework, which is mainly composed of both small and large oysters (Fig. 9D). The large specimens frequently reach a length of 8–9 cm and possibly belong to the genus *Praeexogyra*. This genus contributes to about 3% of the reef framework. *Praeexogyra* is generally observed in a vertical position with upward direction of the umbo and served as a support for the small *Nanogyra nana* Sowerby. The latter oysters form the bulk of the reef structure (48%). They enlarge the pre-existing framework growing one on top of the other in upward, sideward and downward directions. Commonly, new large oysters settle on the existing framework, creating some additional relief. Only their cemented left valves generally represent both oysters. But in some cases, small *Nanogyra* occur with both valves


RE1
A
B
RE3
RE2
2 m
C
1 m
D
1 m
E
RE4
RE3
2 m
F

preserved. A similar *Praeexogyra* - *Nanogyra* association was previously described from deposits of brackish bays and lagoons in the Upper Kimmeridgian/lowermost Tithonian of Portugal (Fürsich 1981). Encrusters on the oysters are relatively abundant and include numerous bryozoans and serpulids. They frequently coat the internal surface of the cemented left valves of *Nanogyra*. About 5.5% of the reef rock is formed by these encrusters together with a thin millimetric crust of microbialites (Fig. 10D, E). Bivalve borings (*Gastrochaenolites*) and voids made by microbioeroders amount to 12% of the reef volume. The remaining volume (37.5%) corresponds to sediments (mudstones to packstones).

In coral-microbialite reefs, corals are the main framebuilders and cemented bivalves generally represent the framework of oyster reefs. Oysters are scarce in RE1 reefs, whereas they may locally be important in reefs of the RE3, RE4, and RE5 types. They correspond to up to 9% of the surface in RE4 and RE5 reefs. Some RE4 reefs are particular in showing numerous cemented bivalves and thus may be called mixed coral–bivalve–microbialite reefs. Framebuilding bivalves probably belong to the genus ? *Eoplicatula* (det. F. Fürsich and W. Werner), but determination remains difficult, because the shells cannot be easily extracted from the substrate. These bivalves are generally observed with both valves connected. They formed isolated, decimetric to metric patches between the coral framework (Fig. 9I) corresponding to up to 33% of the reef volume in RE4 reefs. They were observed at the base and/or at the top of the bioherms.

Main reef components

Corals

Corals are abundant and diverse along the section. They flourished mainly during the 5 successive reef-building events. Only a few massive colonies of *Stylina* were observed outside the reefs in facies 1. In the marly deposits of facies 6, corals are missing. A total of 20 genera of corals were identified in the quarry. Growth forms are phaceloid, ramose, lamellar, dome-shaped, and irregularly massive.

Fig. 5 Morphology of coral-microbialite reefs and oyster reefs (Middle to Upper Oxfordian, Pagny-sur-Meuse). **A** Panoramic view showing the outcrop aspect of a reef formed during the first reef-building event (RE1). This coral-thrombolite reef is more than 200 m wide and about 12 m high with a convex upper surface. The working face is 20 m high. **B** Close-up view of RE1 reef, with a framework of very large colonies of *Aplosmilia* (and *Stylosmilia*). Note the conspicuous erosional surface (*arrow*), which truncates the corals in life position. **C** View of reefs corresponding to the reef-building events RE2 and RE3. The RE2 reefs are small, metric oyster reefs, whereas RE3 reefs are coral-microbialite bioconstructions. **D** Close-up view of RE2 reef, showing a knobby outer surface (*arrow*). Each knob is about 20–30 cm in diameter. **E** Small, metric coral-microbialite patch reef of RE3. **F** The RE3 reef-building event is also characterised by decametric coral-microbialite reefs. Directly above the topographic high created by a larger bioconstruction of RE3 type, several plurimetric to decametric RE4 reefs became established

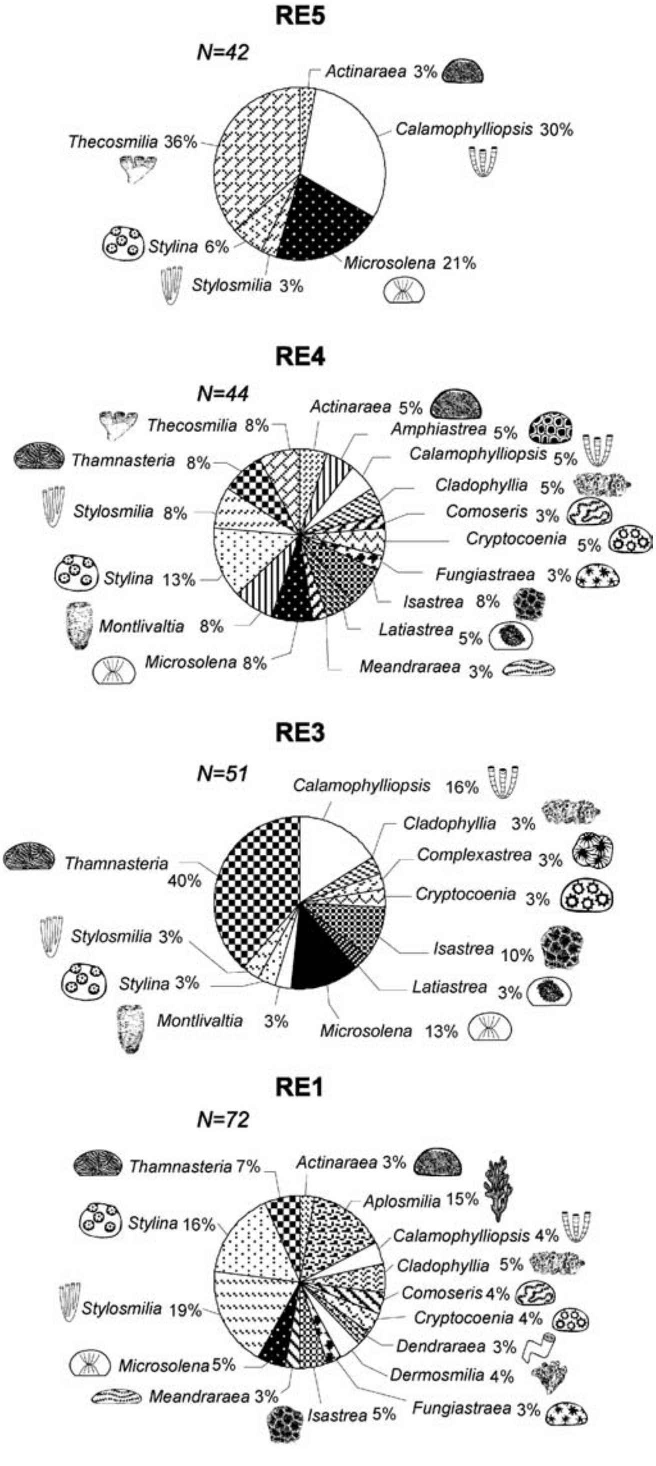
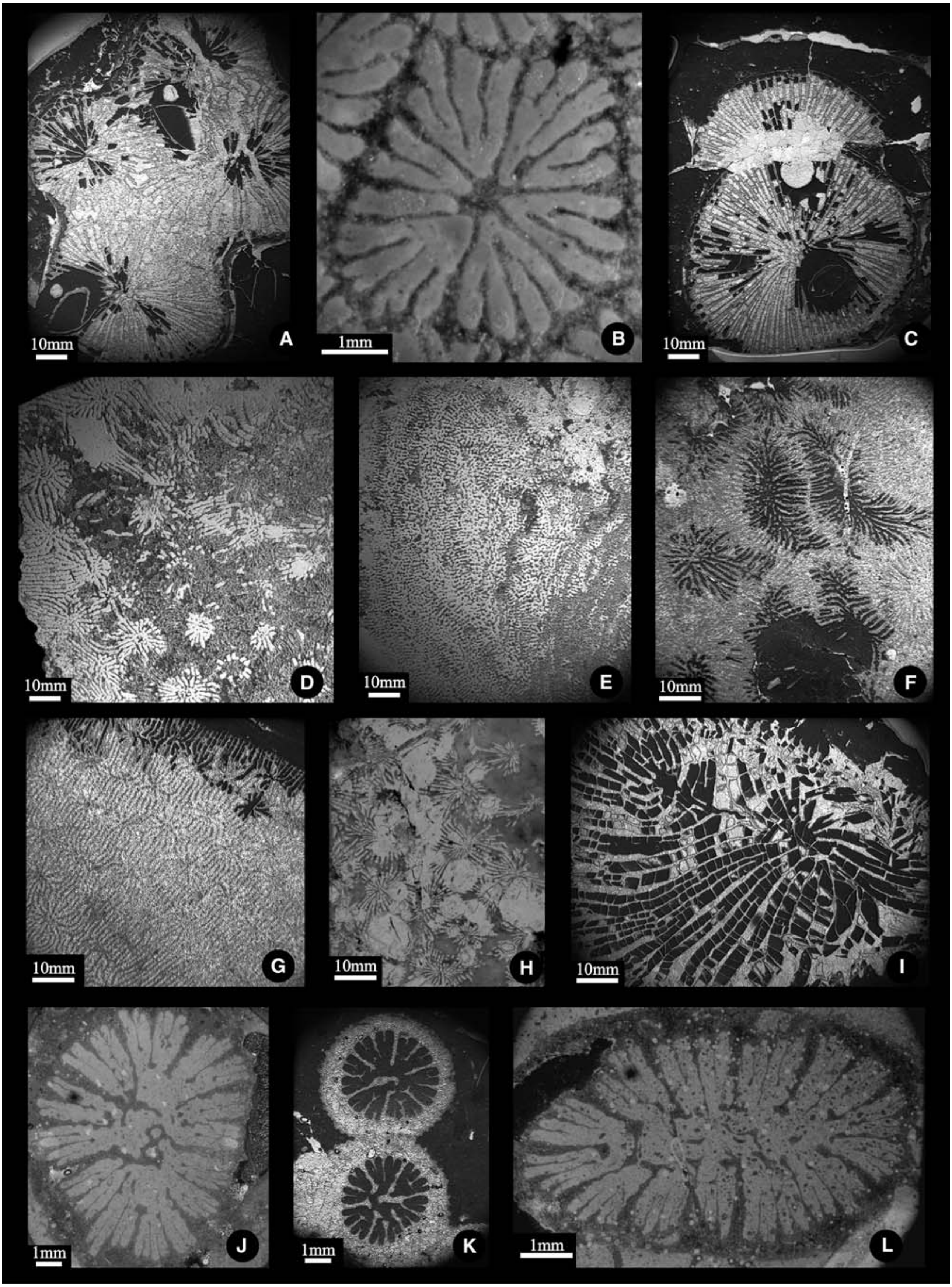


Fig. 6 Distribution of the coral genera in the different coral-microbialite reef-building events studied at Pagny-sur-Meuse (RE1, RE3, RE4, and RE5). *N* number of specimens. Some schemata of corals are adapted from Dupraz (1999)

The RE1 reefs in the part of the section consisting of pure carbonates reveal a relative diverse coral fauna consisting of 15 genera (Fig. 6). In the lower part of the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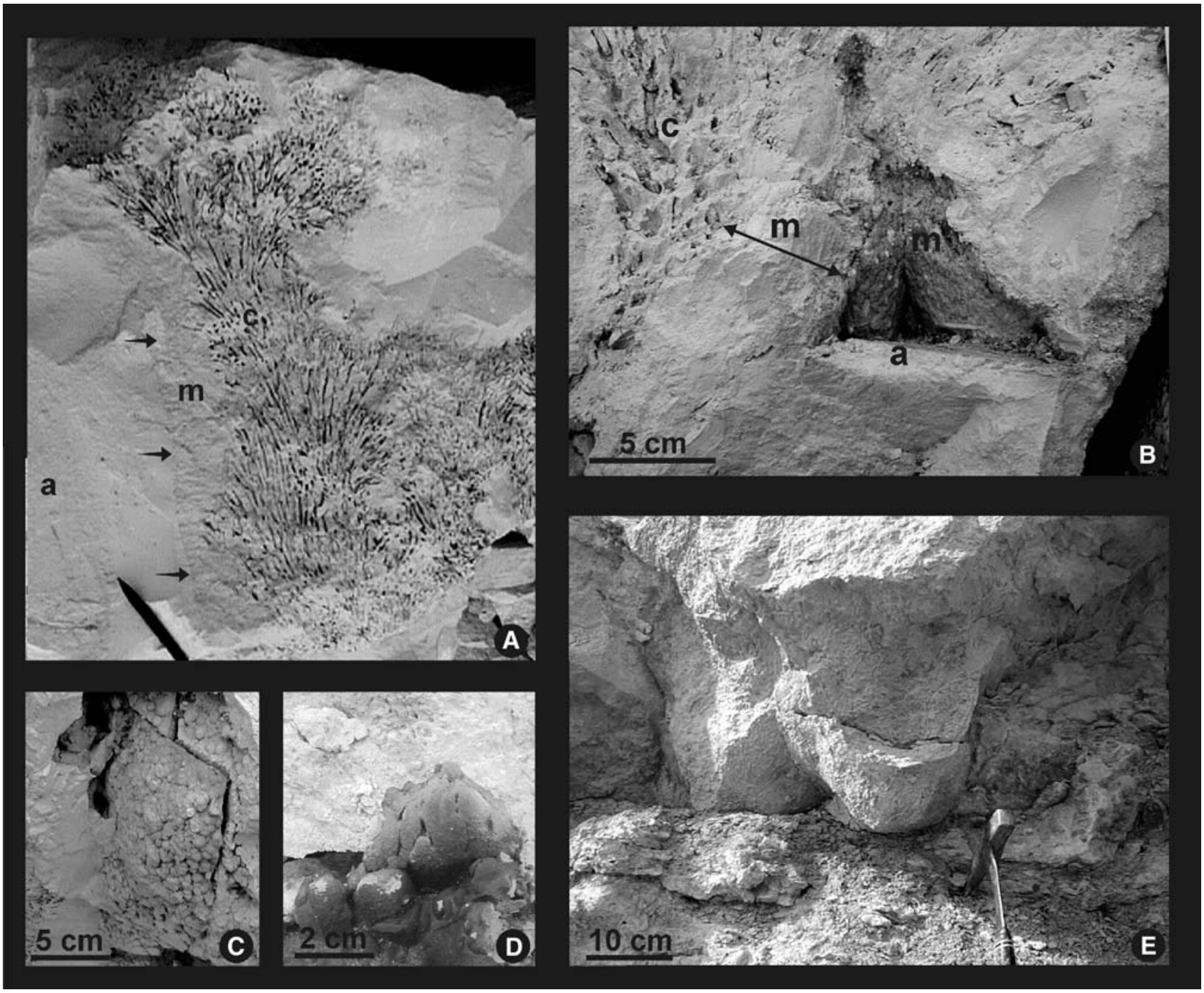
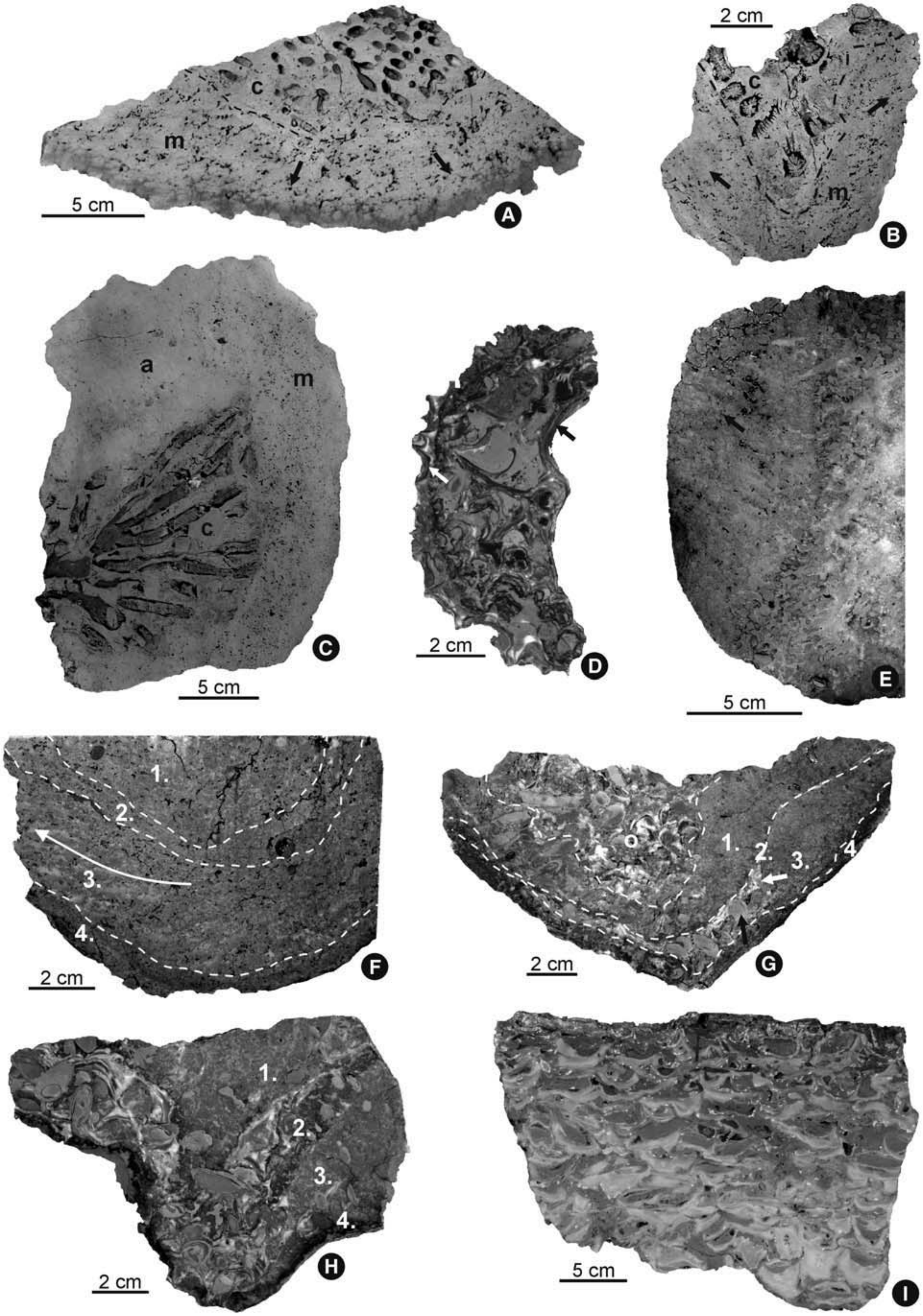


Fig. 8 Close-up views taken in the field depicting microbialitic crusts which have formed during the reef-building events recognized at Pagny-sur-Meuse (Upper-Middle Oxfordian). **A** Large colony of *Stylosmilia* encrusted by a 2–4-cm-thick microbialitic crust. First reef-building event (RE1). Microbialites are only present on the left underside of the coral and are missing on its top. *Black arrows* point to the limit between allomicrite and microbialites. *c* coral; *m* microbialite; *a* allomicrite. *Pencil at the bottom left* of the photo is 5 cm long. **B** Close-up view of a 5-cm-thick microbialitic crust (*black arrow*; *m* microbialite), which covers a colony of *Aplosmilia* (*c*). Microbialitic growth shows a radial direction. Note the allomicrite infilling (*a*) of a small centimetric cavity between two mammilated thrombolitic crusts. Within the cavity, the outer surface of microbialites shows small (up to 1 cm) microbialitic columns. First reef-building event (RE1). **C** Knobby outer surface of a mammilated microbialitic crust from the underside of a bioconstruction. Each knob is 1–3 cm in diameter and corresponds to the end of a microbialitic column. First reef-building event (RE1). **D** Dendroid structure of microbialites, showing an upward growth direction. First reef-building event (RE1). **E** Decimetric mammilated microbialites from the underside of bioherm. Third reef-building event (RE3)

Fig. 7 Corals of the Middle-Upper Oxfordian from the Pagny-sur-Meuse section. **A** Cerioid *Complexastrea* mg. from the western bioherm. Third reef-building event (RE3). Thin section, transversal view. **B** Massive *Amphiastrea* from the fourth reef-building event (RE4). Thin section, transversal view. **C** Dendroid *Thecosmilia* mg. from the western bioherm. Fifth reef-building event (RE5). Thin section, transversal view. **D** Thamnasterioid *Fungiastraea* from the base of the quarry. First reef-building event (RE1). Thin section, transversal view. **E** Massive meandroid *Comoseris* from the first reef-building event (RE1). Thin section, transversal view. **F** *Latiastrea* from the fourth reef-building event (RE4). Thin section, transversal view. **G** Thamnasterioid *Thamnasteria* from the eastern bioherm. Third reef-building event (RE3). Thin section, transversal view. **H** Strongly bioeroded massive cerioid *Isastrea* from the eastern bioherm. Third reef-building event (RE3). Polished slab, transversal view. **I** ?*Latiphyllia* mg. from the western bioherm. Third reef-building event (RE3). Thin section, transversal view. **J** Phaceloid *Calamophylliopsis* from the first reef-building event (RE1). Thin section, transversal view. **K** Phaceloid *Stylosmilia* from the first reef-building event (RE1). Thin section, transversal view. **L** Phaceloid *Aplosmilia* from the first reef-building event (RE1). Thin section, transversal view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outcrop observed, the reef is formed mainly by massive colonies, such as *Isastrea*, *Microsolena* , and *Thamnasteria*. Above these massive corals, phaceloid colonies progressively dominate the reef core with metric *Aplosmilia* and *Stylosmilia* (Fig. 7J, K, L). Large and sturdy *Aplosmilia* are abundant and form 5–10-m high and extensive thickets in the central part of the bioconstruction (Geister and Lathuilière 1991). Delicate *Stylosmilia* represent the most common phaceloid corals, which surround the large stacks of *Aplosmilia*. Large-branching *Calamophylliopsis* and small colonies of *Cladophyllia*, *Dermosmilia* and *Thecosmilia* only occur scarcely. The plocoid *Stylina* is the most common massive coral. Some isolated colonies observed laterally on the reef core, can reach very large dimensions (up to 1.3 m in horizontal diameter; Geister and Lathuilière 1991). A sclerochronological measurement made on a large *Stylina* colony revealed an annual growth rate of 6 to 7 mm/y. Other dome-shaped taxa include *Comoseris*, *Isastrea*, and *Cryptocoenia* (Fig. 7E). Lamellar forms are also present with the genera *Microsolena*, *Thamnasteria*, *Fungiastraea, Actinaraea*, and *Isastrea*, whereas *Microsolena* and *Thamnasteria* are mainly represented by encrusting forms. Ramose corals present a few branching colonies of *Dendraraea* and *Cryptocoenia*.

Fig. 9 Internal structure of microbialite, bivalve and oyster reef elements (Middle to Upper Oxfordian, Pagny-sur-Meuse). **A** Internal structure of a mammilated microbialite from the underside of a bioherm. Phaceloid colony of *Stylosmilia* (*c*). Note the thrombolitic texture (*m*) and the downward growth direction (*black arrows*). First reef-building event (RE1), polished slab. **B** Mammilated microbialite from a bioherm flank. The thrombolitic columns (*m*) on a colony of *Aplosmilia* show a sideward to upward growth direction (*black arrows*). First reef-building event (RE1), polished slab. **C** Mammilated microbialite of bioherm flank. A 5-cm-thick thrombolite (*m*) encrusts a colony of *Aplosmilia* (*c*). Note that the not encrusted upper part of the colony is covered by sediment (*a*). First reef-building event (RE1), polished slab. **D** Internal structure of a centimetric knob from an oyster reef. Note the two types of oysters: ? *Praeexogyra* (*black arrow*) and *Nanogyra nana* (*white arrow*). Second reef-building event (RE2), polished slab. **E** Mammilated microbialite of bioherm flank. Pluricentimetric microbialites made by thrombolitic columns (*black arrow*) encrust a massive colony of *Latiastrea*. Third reef-building event (RE3). Polished slab. **F** Mammilated microbialite from underside of bioherm, showing four thrombolitic growth phases (1–4). Phases 1 and 3 correspond to major microbialitic growth phases and show a thrombolitic texture, whereas phases 2 and 4 show a more massive texture and a reduced thickness. Note that the direction of thrombolitic growth tends to become vertical (*black arrow*). Third reef-building event (RE3), polished slab. **G** Internal structure of a mammilated microbialite from the underside of a bioherm, showing four thrombolitic growth phases (1–4). The growth direction is both downward and sideward from a nucleus made by oysters (*o*) that encrust a coral which is not preserved. The termination of each of the major thrombolitic growth phases (phases 1 and 3) is marked by a more massive and thinner crust (phases 2 and 4). This thin thrombolitic crust is largely overgrown by oysters (*white arrow*) and heavily bored (*black arrow*). Fourth reef-building event (RE4), polished slab. **H** Mammilated microbialite from the flank of bioherm showing 4 microbialitic growth phases. The encrustation started from a coral not visible in this section. Similar to Fig.9b, each major thrombolitic growth phase is marked by a thin thrombolitic layer with *darker colour*, encrusted by numerous oysters and intensively bioeroded. Third reef-building event (RE3). Polished slab. **I** Framework made by the bivalve ? *Eoplicatula*. Fourth reef-building event (RE4), polished slab

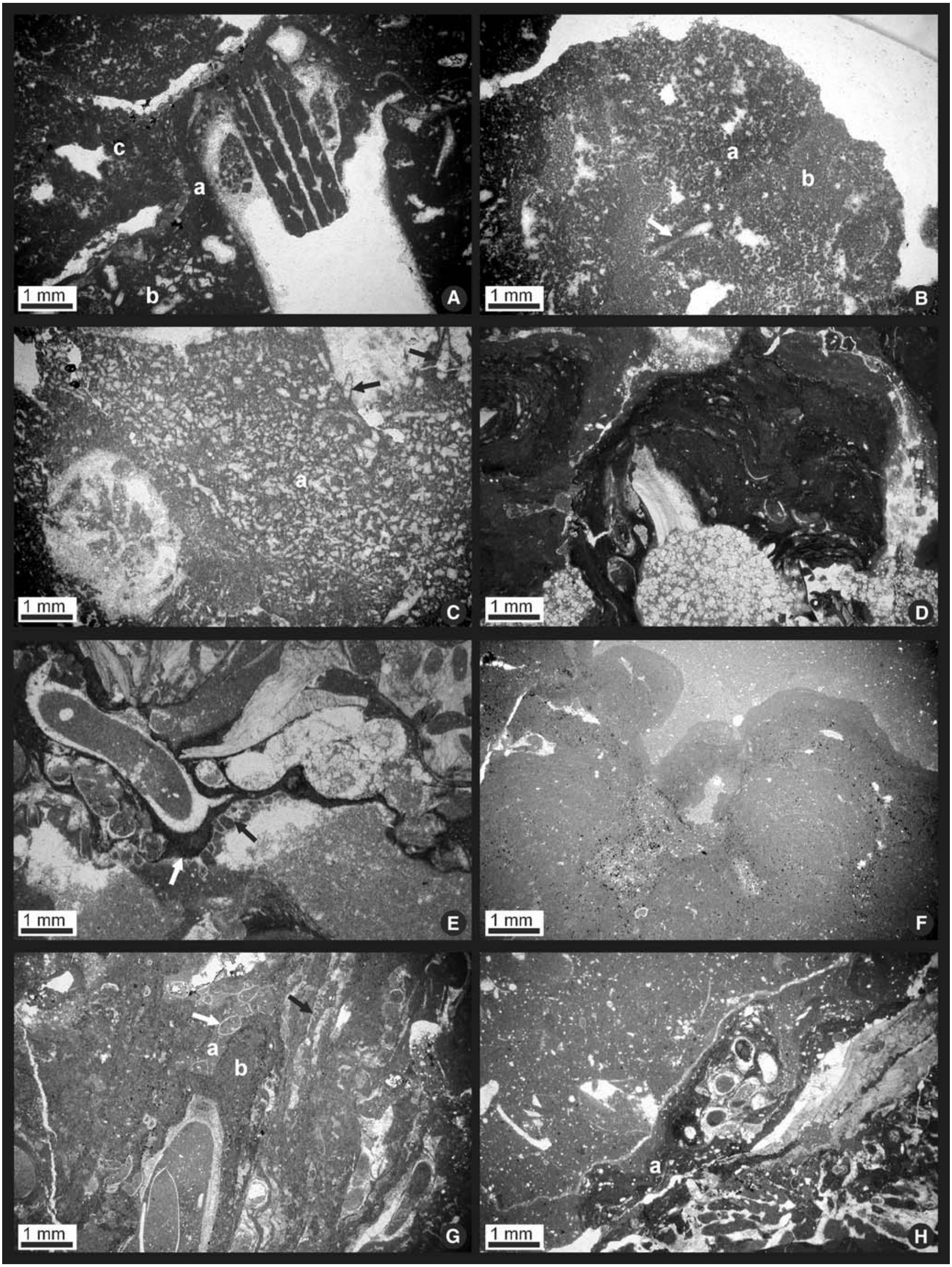
In the mixed carbonate-siliciclastic section, the coral diversity of RE3 reefs is reduced to 11 genera (Fig. 6). Furthermore, the occurrence of these taxa seems to be correlated with the size of the bioconstructions. Small metric patch-reefs are of very low diversity with only 3 genera present (Fig. 11). In these small bioherms, massive colonies are most common with *Thamnasteria* and a few colonies of montlivaltiids, which seem to have ceased growth at an early phase of their astogeny (Fig. 7A). These corals include various morphogenera of colonial forms such as *Complexastrea* (and ? *Lathophyllia* mg., Fig. 7I; see Lathuilière 1996a), but also rare solitary *Montlivaltia* and budding *Montlivaltia* are present. The latter are similar to those observed by Lathuilière (1996a, 1996b) in Middle Jurassic beds. By contrast, branching colonies are not observed in these metric bioherms. On the other side of the quarry, a much larger bioherm is more diverse with 9 genera. Massive colonies always dominate the coral fauna. The most common taxa encountered are the genera *Microsolena* and *Isastrea*. *Thamnasteria* is still present, having secondary importance compared to other massive forms (i.e. *Cryptocoenia* and *Stylina*). *Stylosmilia*, *Cladophyllia*, and *Calamophylliopsis* represent phaceloid taxa, but these are not very abundant.

RE4 reefs with 16 genera identified so far, have a higher diversity than RE3 reefs and are thus comparable to RE1 reefs. *Stylina* is the most common taxon here (Fig. 6). The sclerochronological measurement of a specimen of *Stylina* revealed an annual growth rate ranging from 9.12 to 11.11 mm/year. Other massive corals include *Microsolena*, *Latiastrea*, *Cryptocoenia*, *Amphiastrea*, *Comoseris*, *Fungiastraea*, *Actinaraea*, and *Meandraraea*. Phaceloid *Stylosmilia*, *Cladophyllia*, and *Calamophylliopsis* are always sporadically found (Fig. 7B, F).

The small patch reefs of RE5 are of low diversity with only six genera found. Phaceloid forms of *Thecosmilia* and *Calamophylliopsis* are most common (Fig. 7C) and are associated with a few *Stylosmilia* colonies. *Microsolena* is also well represented, whereas other massive taxa such as *Stylina* and *Actinaraea* are only of secondary importance.

Microbialites

Microbialites are present both in the carbonate-dominated and in the mixed carbonate-siliciclastic part of the section. The microbialitic crusts show a clotted mesostructure characteristic of thrombolites (Aitken 1967; Kennard and James 1986; Shapiro 2000), and locally of leiolites (Braga et al. 1995). Microscopically, they can show three main types of microfabrics (Leinfelder et al. 1993; Riding 2000): dense, clotted, and peloidal micrites (Fig. 12). Microbialites are moderately to abundantly developed and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form a 3–8-cm-thick crust on corals and other skeletons, constituting the primary framework (Figs. 8 and 9).

In RE1 reefs, microbialites are moderately well developed and represent about 16% of the reef body. A thin layer of thrombolites (up to 5 cm thick) generally encrusts colonies of branching and massive corals. At the mesoscopic scale, these crusts show a light colour similar to sediment coloration, making distinction difficult (Fig. 9A, B, C). Thrombolites appear to be able to develop on various skeletal components (e.g. corals, brachiopods, and bivalves) encountered in the reef body. However, they are not homogeneously distributed in the reef framework. Some high-standing phaceloid colonies such as *Aplosmilia* and *Stylosmilia* show a crust on their underside, whereas a crust is lacking on their upper surface (Fig. 8A). Lamellar colonies (e.g. *Thamnasteria*) and other encrusting fauna (e.g. brachiopods) can also be devoid of microbial crusts. Microbialites show morphologies that are similar to those observed in other Oxfordian or Kimmeridgian reefs (Leinfelder et al. 1993; Bertling and Insalaco 1998; Olivier et al. 2003; Olivier 2004). Mammilated microbialite morphologies are frequently observed on phaceloid corals. As seen in sections, this type of microbialite reveals a relative homogeneous and continuous structure formed by thrombolitic columns, which indicate various growth directions. Lateral to vertical growth is characteristic of mammilated microbialites on bioherm flanks, whereas downward to sideward growth formed mammilated microbialites on bioherm undersides (Fig. 9A; Olivier et al. 2003). Microbialites on undersides can show a typical knobby outer surface (Fig. 8C). Each knob is about 0.5–2 cm across and corresponds to the ends of many thrombolitic columns. The microbialites on the flanks show a knobby outer surface in their lower part and a columnar outer surface in their upper part (Fig. 8B). In some small centimetric to decimetric cavities, thrombolites developed atypical globular to dendroid growth forms (Fig. 8D). Thrombolites can also form 1–3-cm-thick and relatively flat crusts on the upper surface of lamellar corals, but they are lacking on the lower coral surface. At the microscopic scale, thrombolites form a typical crust of two layers, as observed in Oxfordian coral-thrombolite reefs elsewhere (Dupraz and Strasser 1999, 2002). A thin inner layer consists of dense micrite, more or less laminated and directly encrusted onto the coral surface (Fig. 10A). This crust is laterally not continuous and generally shows a flat to wavy upper surface. The second layer is generally formed by peloidal, locally clotted micrite resulting in pluricentimetric columns of thrombolites (Fig. 10B).

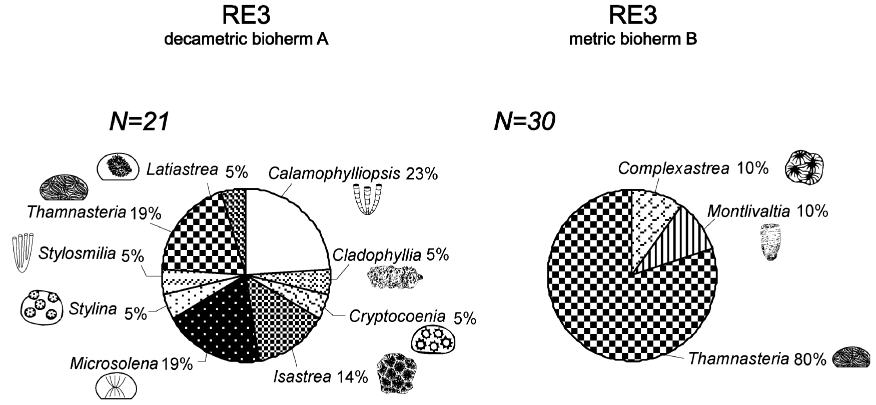
Fig. 10 Microstructure and micro-encrusters (Middle to Upper Oxfordian coral-microbialite and oyster reefs, Pagny-sur-Meuse). **A** Longitudinal section of *Stylosmilia* with alternating auriculae showing a millimetric crust of dense micrite (*a*) with a few nubeculariids. This first microbial layer also encrusts *Bacinella irregularis* (*b*) and is overgrown by a second, centimetric microbial crust made of peloidal micrite (*c*). First reef-building event (RE1), thin section. **B** Columnar thrombolite consisting of peloidal micrite (*a*). *Terebella* (*white arrow*) generally encrusts the microbialitic columns. Remaining space between the columns is filled by a micritic or bioclastic matrix (*b*). First reef-building event (RE1). Thin section. **C** Transversal section of two branches of the phaceloid ? *Stylosmilia*, perforated by the foraminifer *Troglotella incrustans* (*black arrows*). The encruster *Bacinella irregularis* (*a*) fills all the space between the branches. First reef-building event (RE1), thin section. **D** Domes of dense to clotted micrite with numerous nubeculariids. The crust mainly developed on the upper surface of a bored oyster shell. Second reef-building event (RE2), thin section. **E** Dense micrite (*white arrow*) encrusting oysters and serpulids. A bryozoan (*Plagioecia*, *black arrow*) became established directly on this microbial layer. Second reef-building event (RE2), thin section. **F** Columns of clotted to micropeloidal micrite. Third reef-building event (RE3), thin section. **G** Encrustation showing several successive phases of dense to clotted micrite overgrown by numerous bryozoans (*black arrow*) and serpulids. Note *Bullopora* (*white arrow*). Bioclastic matrix (*a*) filled the space between small columns of dense to clotted micrite (*b*). The growth direction of the crust is both sideward and upward. Mammilated microbialite from the flank of a bioherm. Third reef-building event (RE3). Thin section. **H** Typical microbialitic crust formed in two layers. Dense micrite (*a*) with numerous nubeculariids overgrowing coral, oyster, and serpulids. Fourth reef-building event (RE4). Thin section

In the marly level of facies 4, microbialites form only a low proportion (<4% of the volume) of the oyster patch reefs. At the macroscopic scale, microbialitic crusts are generally very thin (a few millimetres) and of light-brownish colour. They are directly encrusting oyster shells, bryozoans, and serpulids. At the microscopic scale two different kinds of microbial micrite can be recognized:

1. A very thin and dark layer of dense micrite that does not exceed 0.5 mm in thickness and shows a planar upper surface (Fig. 10E). Lamination is rare here. This layer is generally best developed on the inner side of cemented left oyster valves, but is also present on the free right valves.
2. A layer formed by dense to clotted micrite showing an irregular to domal upper surface with a lamination more or less well developed (Fig. 10). This layer either directly encrusted its supports (e.g. oyster valves, serpulids, and bryozoans), or it is found in continuation of the dense micrite previously described. It is not observed on the lower surface of various reef supports and generally shows an upward growth direction. This crust can reach up to 3 mm in thickness.

In mixed carbonate–siliciclastic deposits of facies 5 and 6, microbialites are largely represented in both RE3 reefs (with about 25–35%) and RE4 reefs (with 16% of the reef body volume). They are most abundant in RE5 reefs (55%). At the macroscopic scale, they show a colour darker than the sediment and usually form microbialites on flanks and undersides of bioherms (Figs. 8E and 9G). The relief of mammilated microbialites can reach 25 cm in diameter. Microbialites developed on various supports such as branching, dome-shaped and lamellar corals, or on other skeletal components like framebuilding bivalves. They generally show a classic internal structure with an outer layer made by thrombolitic columns (up to 5 cm long) and an inner layer composed of more massive

Fig. 11 Lateral variation of coral assemblages observed in two RE3 reefs of different size: a decametric reef (**A**) and a metric reef (**B**)



thrombolites (up to 3 cm thick). Such an internal organisation of microbialites was previously described from Holocene and Kimmeridgian coral-thrombolitic reefs (Montaggioni and Camoin 1993; Camoin and Montaggioni 1994; Camoin et al. 1999; Olivier et al. 2003). However, some mammilated microbialites commonly show several generations of thrombolite growth (Fig. 9F, G, H). Each growth phase is formed by a succession of a typical thrombolitic crust, 1–5-cm-thick with a thin but dense outer thrombolitic layer. This latter is thinner (0.5–1 cm thick) and was heavily bored. Oysters, of which only the cemented left valve is preserved, encrust it. Another microbialite structure on the upper surface of lamellar corals is a 1–2-cm-thick dome-shaped crust with a leiolitic fabric. Few specimens of the lamellar corals have a microbialitic crust on both their lower and upper surfaces. The upper surface shows centimetric columns of thrombolite with upward growth, whereas the lower surface shows a thin (about 1 cm thick) and dense crust with downward growth. Although decimetric intrareef cavities were not found in the outcrops themselves, some quarry blocks revealed centimetric (up to 5 cm long) thrombolitic columns with upward growth. Such an internal structure is very similar to that observed in pseudostalactitic microbialites in cavities of some Oxfordian and Kimmeridgian coral-microbialite reefs (Bertling and Insalaco 1998; Olivier et al. 2003). At the microscopic scale, two successive micritic crusts form microbialites with two distinct fabrics:

1. A thin, millimetric layer of dense micrite, generally not continuous, with a flat to irregular upper surface (Fig. 10H). Numerous nubeculariids that settled directly on the corals can be associated with this crust.
2. A second layer corresponding to two main types of micrite—peloidal micrite and clotted micrite. Peloidal micrite mainly occurs when microbialites are mesoscopically of columnar shape (Fig. 10F). In that case, micro-encrusters are rare and lamination is not frequent. Clotted micrite (sometimes clotted to dense) occurs in mesoscopic microbialites with a more massive texture. These show several growth phases of microbialites and domal to small columnar structures (Fig. 10G), and they can appear densely laminated and are frequently overgrown by various and numerous micro-encrusters (mainly oysters, bryozoans, and serpulids).

Micro-encrusters

Micro-encrusters are commonly associated with the microbialites. Their composition is quite similar to micro-encrusters encountered in Upper Jurassic coral-microbialite reefs elsewhere (Leinfelder et al. 1993; Schmid 1996; Dupraz and Strasser 1999, 2002). In a pure carbonate setting, the encrusting organisms of RE1 reefs are characterised by locally abundant *Bacinella irregularis* Radoicic and some *Lithocodium aggregatum* ELLIOT (10A, C). However, *Terebella lapilloides* MÜNSTER remains the most abundant micro-encruster (Fig. 13). Some nubeculariids, rare *Tubiphytes*, and *Bullopora* are also observed. Calcareous sponges and serpulids occur sporadically. In the mixed carbonate-siliciclastic environments, the composition of micro-encrusters remains relatively constant throughout all the coral-microbialitic reef-building events under discussion. *Terebella*, nubeculariids and serpulids are the three most abundant micro-encrusters (Figs. 10G and 13). The foraminifer *Bullopora*, bryozoans and thecideid brachiopods are also largely represented. Small calcareous sponges are always present and siliceous spicules are scarcely observed. In RE2 reefs, bryozoans (*Plagioecia*) and serpulids (*Tetraserpula* and *Cycloserpula*) abundantly encrust oysters (Fig. 10E). Nubeculariids were rarely observed (Fig. 10).

The different micro-encrusters show a preferential distribution related to other reef components. Generally, nubeculariids and *Tubiphytes* are associated with the first inner micritic crusts. *Terebella* and *Bullopora* rather encrust clotted to peloidal micritic columns. Bryozoans and calcareous sponges are observed encrusting both the coral surface and the first dense micritic crust. Thecideid brachiopods are also found on the microbialite surfaces of RE3, RE4, and RE5 reefs. Serpulids and small oysters seem to settle on all types of support (i.e. corals and microbialites). *Bacinella* and *Lithocodium* are always observed forming encrustations directly on the coral surfaces of RE1 reefs.

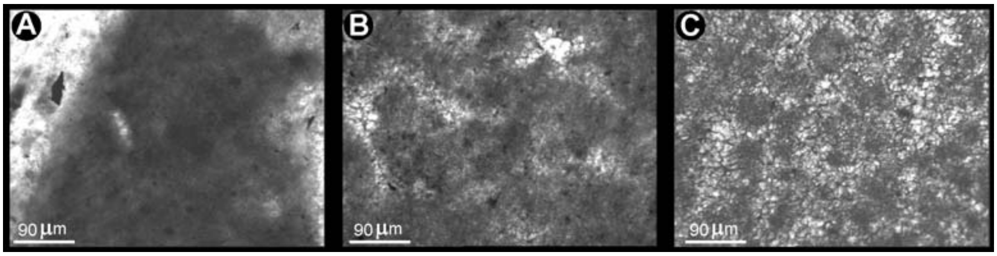


Fig. 12 Photomicrographs of the three main micritic fabrics observed in coral-microbialite reefs of Pagny-sur-Meuse. **A** Dense micrite encrusting an oyster shell (*upper left corner*). This type of micrite can also show an important lamination with numerous nubeculariids. **B** Clotted micrite. **C** Peloidal micrite

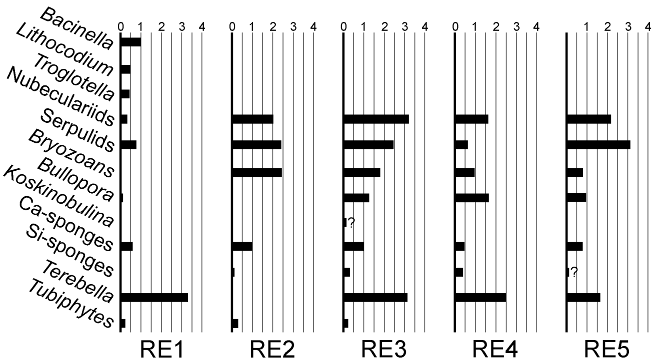


Fig. 13 Distribution of principal micro-encrusters associated with microbialites in the successive reef-building events of the Pagny-sur-Meuse section. *0* not observed; *1* rare; *2* present; *3* common; *4* abundant. *Ca-sponge* calcareous sponge; *Si-sponge* siliceous sponge

Discussion

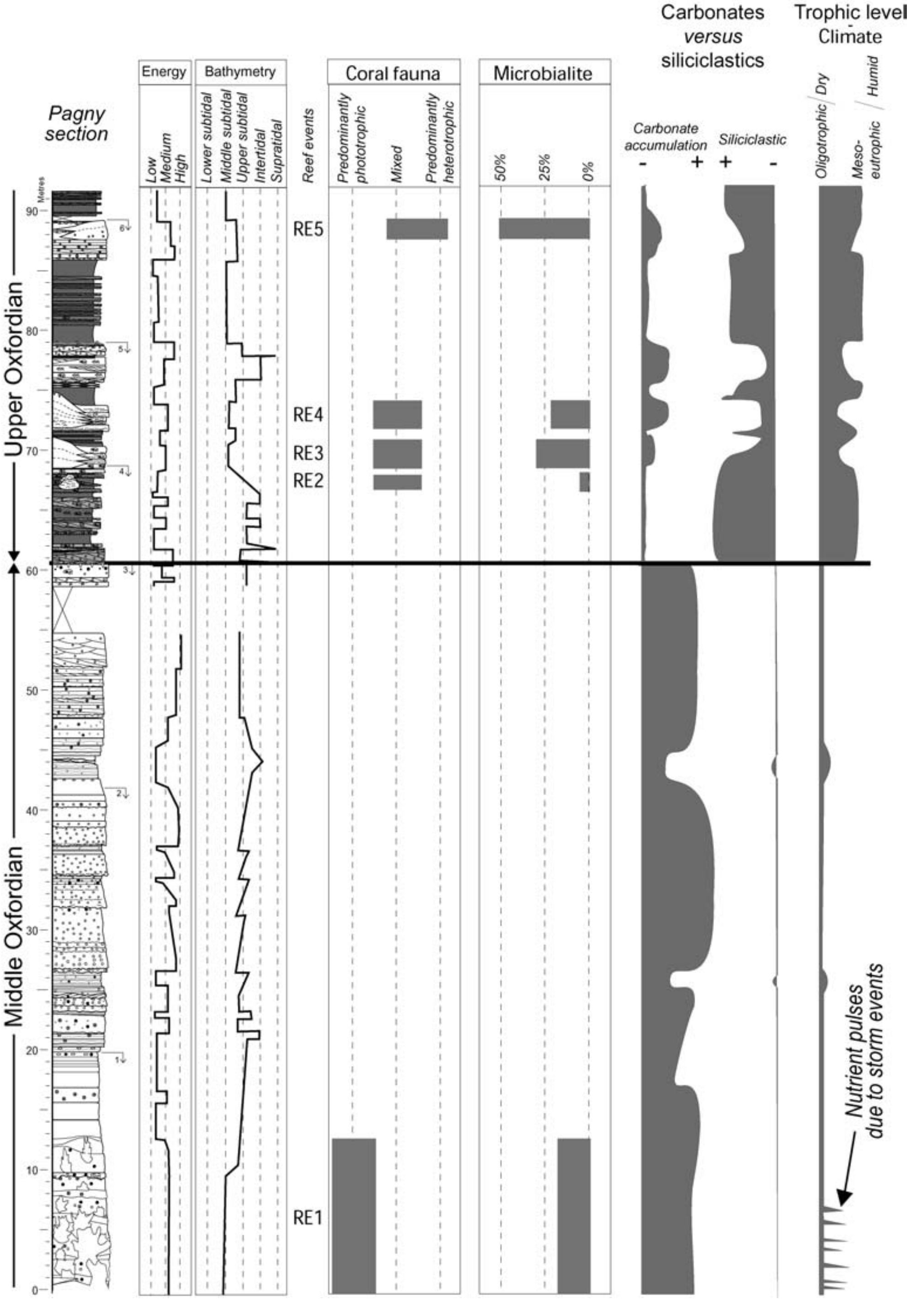
Distribution and significance of reef-builders

Coral associations and depositional environments

With 20 genera identified, the coral fauna of Pagny-sur-Meuse is rather diverse and similar to that observed in the Middle Oxfordian coral-microbialite reefs of the Swiss Jura (Dupraz 1999; Dupraz and Strasser 1999, 2002), and of the eastern Paris Basin (Beauvais 1964; Bertling and Insalaco 1998). The coral fauna is of considerably higher diversity than that of the Middle Oxfordian of England (Insalaco 1996, 1999; Insalaco et al. 1997). It is suggested that this distribution pattern is of climatic origin and related to a paleolatitudinal thermal gradient (Cecca et al. 2001, Martin-Garin et al. 2002). In the depositional environments observed at Pagny-sur-Meuse, both the various colony shapes (lamellar, branching, and dome-shaped) and the diversity of colonial structures (phaceloid, cerioid, thamnasterioid, and plocoid) do not seem to be affected by the transition from pure carbonate to mixed carbonate-siliciclastic environments. However, this abrupt change in the depositional environment had a direct influence on the taxonomic composition of the coral associations themselves (Fig. 6).

In pure carbonate settings, RE1 reefs are relatively diverse with their 15 genera and are dominated by an association of very large *Aplosmilia* and stylinids (*sensu* Gill 1977). The low equitability and the qualitative assessment of the coral cover suggest that this assemblage does not represent an optimal environment in spite of the diverse coral fauna present (Dupraz and Strasser 2002). The association is probably controlled by moderate environmental stress. Diversity and analysis of shape and size of colonies suggest that light and temperature are not limiting factors. A considerable input of sediments could explain the high proportion of branching and plocoid forms such as *Aplosmilia*, *Stylosmilia*, and *Stylina*. It is generally accepted that in recent and Jurassic coral reefs, high sediment accumulation generally favours the development of branching forms, (e.g. Roy and Smith 1971; Roniewicz and Roniewicz 1971; Hubbard and Pocock 1972; Hubbard 1973; Zlatarski and Martínez Estalella 1982; Geister and Lathuilière 1991; Rice and Hunter 1992; Leinfelder 1994; Nose 1995; Nose and Leinfelder 1997; Lathuilière 2000a, 2000b), especially when corals are devoid of microbialitic crusts (Nose and Leinfelder 1997). However, numerous well-developed microbialites encrust the underside of some parts of the reef bodies. This clearly indicates a relatively long period from the upgrowth of a coral to its burial by sediments. Thus, microbialitic growth indicates that accumulation rate varied through time. Even though phaceloid corals are well adapted to burial by sedimentation due to their high relief, they do not develop a positive relief on the sea floor in response to sediment accumulation stress. Regional considerations as well as comparison of fauna with other settings (Euville, Dompcevrin and Haudiomont; cf. Lathuilière et al. 2003; Carpentier 2004) suggest that RE1 reefs are representative of a lagoonal environment (Geister and Lathuilière 1991; Vincent 2001). In this depositional setting, periods of high sedimentation rate could lead to a temporary rise in turbidity due to hydrodynamic events. Violent storms or hurricanes capable of severe breakage of coral colonies sometimes interrupted a regime of moderate wave energy. Reiterations of growth after storm events were observed (see also Laternser 2000). The very low portion of pennular filter-feeding corals coincides with a high portion of *Aplosmilia* and stylinids. This suggests that the RE1 association characterises oligotrophic conditions (Fig. 14).

Fig 14 Stratigraphic changes in depositional settings (bathymetry and energy), main coral groups (phototrophic to dominantly heterotrophic) and microbialite abundance in the reef events of Pagny-sur-Meuse (Middle to Upper Oxfordian, northeastern France). Reef development and composition are mainly explained by the combined impact of trophic conditions (climate) and terrestrial run-off. See text for more explanations



In the mixed carbonate-siliciclastic settings of RE3 reefs, increase of terrigeneous input is correlated with a decrease in diversity from 15–11 genera. Stylinids are less well represented, whereas *Thamnasteria* and *Microsolena* dominate. *Thamnasteria* is known for its very large ecospace (Bertling 1993, 1995) and has been signalled for its pioneering capability to recolonize habitats after storms (Lathuilière 2000b). *Microsolena* and pennular corals in general are known as suspension-feeders (Lathuilière and Gill 1995). The ecological niche of these corals is either the outer slope of reefs (Geister and Lathuilière 1991; Insalaco 1996) or the lagoon (Dupraz 1999; Dupraz and Strasser 2002). In both cases, environmental settings deviate from the optimal oligotrophic situation of the reef crest. Decrease of the number of stylinid genera in RE3 reefs is probably due to environmental deterioration as a result of terrestrial run-off and to the higher fertility found in waters enriched in nutrients (Fig. 14). However, due to the limited number of samples taken, definite statements are difficult on the true diversity of stylinids in RE3 reefs in comparison to the RE4 reefs, both of which developed laterally on facies 2. At least, the qualitative evaluation in the field clearly shows that the giant colonies of *Stylina* observed in RE1 reefs are absent in RE3, RE4, and RE5 reefs. The lateral variability in coral composition between the different bioherms of RE3 is notable. Small metric bioconstructions appear drastically reduced in diversity with only three genera present (*Thamnasteria*, *Complexastrea*, and *Montlivaltia*), whereas larger bioherms show a definitely higher diversity with 9 genera recognised (Fig. 11). Such variation in the composition of bioconstructions of different sizes was already observed in the recent reefs (Geister 1983).

In RE4 reefs, some assemblages are well-balanced between stylinids (*Stylina* and *Stylosmilia*), microsolenids (*Microsolena*, *Comoseris* or *Meandraraea*) and diverse massive forms (such as *Isastrea, Cryptocoenia and Amphiastrea*). Breakdown of *Calamophylliopsis* and tumbling of *Stylina* is frequent. The relatively higher diversity of RE4 reefs (16 genera) indicates a balanced heterotrophic/phototrophic mode of nutrition (Dupraz and Strasser 2002). Both the coral associations of RE3 and RE4 reefs and the lateral deposits of facies 2 reflect a shallow depositional environment of moderate energy, which was under the influence of recurrent terrigeneous input and frequent storm events.

The framework of the last reef-building event (RE5) is of low diversity with only 6 genera present. The great abundance of *Calamophylliopsis* and *Thecosmilia* might be due to a higher energy environment as previously suggested by the analysis of facies 3. The genus *Calamophylliopsis* is considered to be well-adapted to conditions of heavy sedimentation (Leinfelder et al. 1996) and seems also capable to cope with agitated water (Olivier et al. 2003). *Microsolena* is also well represented and points to a higher fertility than that expected in RE4 reefs. This may be due to an increase in eutrophication linked to terrigeneous input. Thus, RE5 reefs appear to have lived in nutrient-rich waters (fully mesotrophic conditions) of a shallow high-energy lagoon (Fig. 14).

Microbialites and associated micro-encrusters

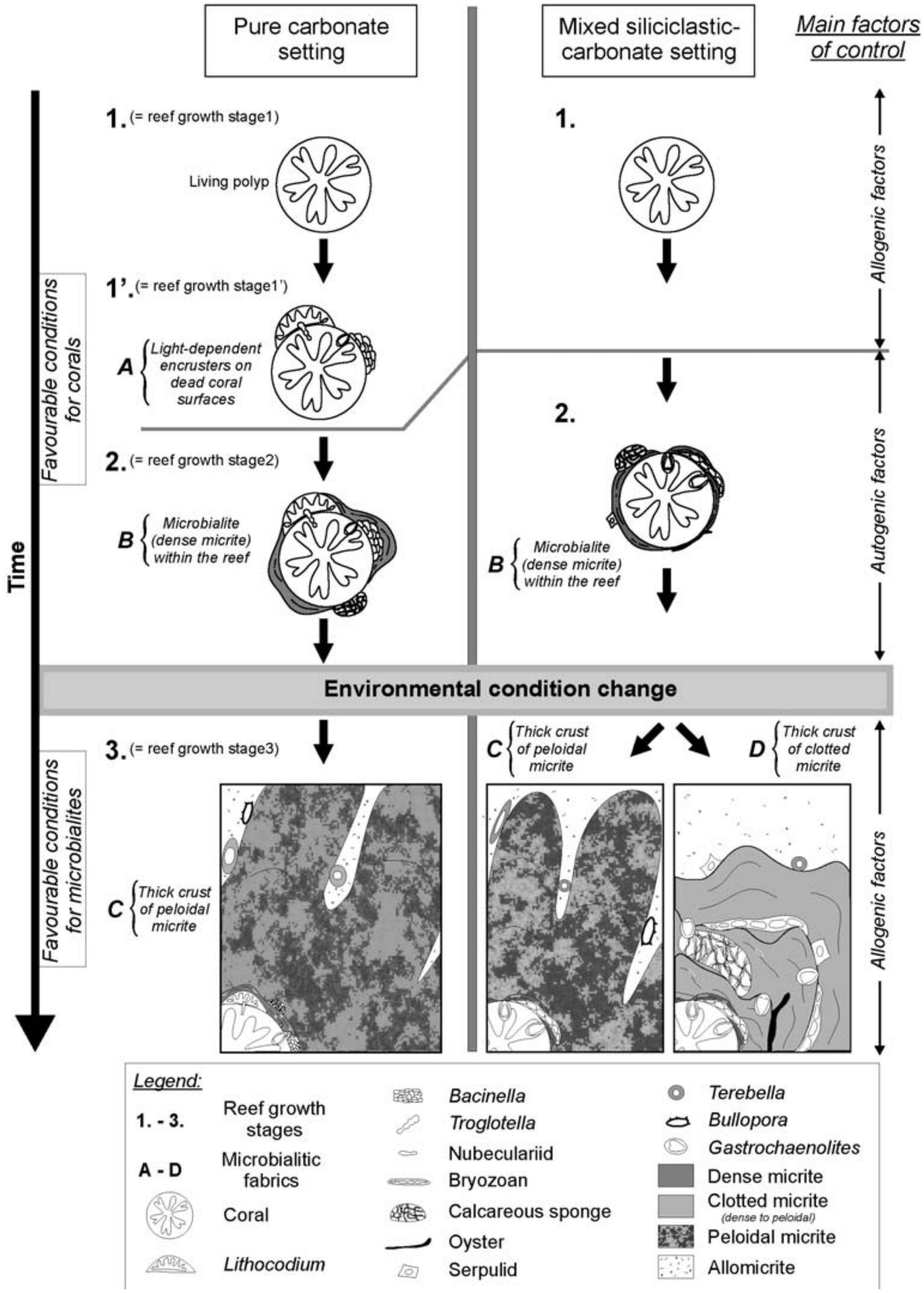
Microbialites are well known from Upper Jurassic coral reefs (see Leinfelder and Schmid 2000). Microbialites can play both reef-building and binding roles (Leinfelder et al. 1996; Olivier et al. 2003). In RE2 reefs, microbialites are very thin and cover indifferently all components of the oyster reefs (e.g. oysters, serpulids, and bryozoans), being essentially binding agents. Such a microbial crust was probably strengthening the oyster framework in an environment frequently disturbed by storm events or tidal currents. In coral-microbialite reefs, the dense micritic crust covering simultaneously several framework components is not observed due to the generally high dimension and relief of the support. But it is generally encrusting a single coral branch or a shell. Thus, binding by dense micrite was probably negligible. On the other side, pluricentimetric peloidal columns emphasize the predominant constructional role played by microbialites in these Upper Oxfordian coral reefs.

It is generally accepted that sedimentation rate and water energy are the two main factors controlling the mesoscopic growth form of microbialites (Braga et al. 1995; Schmid 1996). Parcell (2002) also emphasizes the role played by the rate of sea-level change that directly affects the sedimentation rate. This must be very low for dense microbial development (Sun and Wright 1989; Dromart 1992; Leinfelder et al. 1993). Sedimentological analysis of the Pagny section revealed that sea-level variations probably did not exceed a few metres and thus cannot be considered to be a major control of microbialite growth. Water energy can change between the different reef-building events (Figs. 4 and 14; see also facies 1, 2, and 3), but does not influence the microbialitic crusts. Probably microbialites are mainly controlled by the trophic conditions that prevailed during the reef growth, by their position within the reef structure (i.e. light dependence; Olivier et al. 2003) and by the sedimentation rate (Reitner 1993; Leinfelder et al. 1993; Schmid 1996; Parcell 2002).

At Pagny-sur-Meuse, microbialites are moderately well-developed in RE1 reefs (i.e. laterally on the pure carbonate sediments of facies 1) and are most abundant in mixed carbonate-siliciclastic settings (i.e. RE3, RE4, and RE5 reefs laterally on facies 2 and 3). They are scarcely developed in the oyster reefs that formed in argillaceous environments (facies 6; Fig. 14). These observations suggest that microbialites preferred carbonate environments with a low to moderate siliciclastic content as compared to pure carbonate conditions, and that periods of heavy argillaceous sedimentation were probably not favourable for full microbial development (Dupraz 1999; Dupraz and Strasser 1999, 2002).

Internal structures and fabrics, as well as outer surfaces of microbialites show similarities and differences between a pure carbonate setting and mixed carbonate-siliciclastic environments. At the microscopic scale, the transition from a first millimetric layer of dense micrite to a second centimetric layer of clotted to peloidal micrite probably reflects periods of environmental change, which in these two depositional settings favoured microbial development and carbonate precipitation (Fig. 15). Generally, the first dense micritic layer grew directly on corals and/or oysters that formed the primary framework, as well as on the first generation of micro-encrusters (i.e. *Lithocodium* and *Bacinella*; stages 1, 1' and 2, Fig. 15). These latter are thought to be photophilic microorganisms (Leinfelder et al. 1993; Schmid 1996). Even if this microbial crust is not continuous, it developed both on the upper and lower surfaces of its support. In addition, it is generally overgrown by bryozoans, nubeculariids, calcareous sponges, and oysters. Such a dense micrite layer probably formed just below living coral colonies in somewhat less-illuminated environments (Dupraz and Strasser 1999, 2002). This layer is thought to be confined to areas of low sedimentation rate similar to those observed in the modern

Fig 15 Scenarios of encrustation (i.e. microbialites and micro-encrusters) related to main factors of control (autogenic vs. allogenic) in pure carbonate and mixed carbonate-siliciclastic depositional settings. Note that microbial crust formation can be both autogenically and allogenically controlled. See text for more explanations



reefs of Lizard Island (Reitner 1993). Dense micrite is most abundant in RE2 reefs and is frequently associated with the bryozoan *Plagioecia*. This frequent overgrowth reaction between microbial mats and bryozoans indicates a possible antagonism and/or relationship of commensalism similar to that recently found in modern environments (Scholz and Krumbein 1996; Scholz et al. 2000), and that supposedly has occurred in the Messinian (Moissette et al. 2002). Commensalism relationships can also be observed between numerous nubeculariids growing on dense micrite and on *Tubiphytes morronensis* Crescenti. The latter is interpreted as a miliolid with autotrophic microbial exosymbionts, helping in producing the outer layer (Schmid 1995).

The second micritic layer of microbialites shows two types of texture (stage 3, Fig. 15). The first texture corresponds to the peloidal type (peloidal and/or clotted micrite) that formed mesoscopic columnar microbialites. This microfabric, mainly peloidal, forms almost all the microbial deposits in pure carbonate settings (RE1 reefs) and is also locally observed in microbialites of RE3, RE4, and RE5 reefs. Columns of peloidal micrite can show diffuse lamination and are encrusted by a low-diversity community of microorganisms (i.e. *Terebella* and *Bullopora*). This encrusting fauna is generally interpreted as consisting of sciaphilic organisms and organisms adapted to low-oxygen conditions (Fürsich and Werner 1991; Schmid 1996). These encrusters probably developed in cryptic environments located between the microbialitic columns. Mesoscopically, this peloidal to clotted micrite may form microbialitic crusts with a massive, thrombolitic inner layer and a columnar outer layer. This change in the microbialitic mesostructure could be related to the disruptive influence of particles of allochthonous mud on biofilms, in response to an increase of the sedimentation rate (Reitner 1993). The second texture observed in the second microscopic layer of microbialites is of the clotted type, which shows a general dome-shape or the shape of small columns. It is mainly observed in reefs of RE3, RE4, and RE5 and only rarely found in RE1 and RE2 reefs. It has a relatively dense lamination and is frequently overgrown by abundant nubeculariids, bryozoans, calcareous sponges, and oysters. Mesoscopically, this micritic crust shows several interruptions of growth associated with strong bioerosion and encrustation. All these observations suggest a higher growth rate and more continuous growth for the peloidal type of micrite than for the dense and clotted types.

In Upper Jurassic coral reefs, microbialites developed highly diverse morphologies (Schmid 1996; Olivier et al. 2003; Olivier 2004). The presence of mammilated microbialites at the undersides of bioherms and flanks clearly shows the existence of a sideward and a downward growth direction of thrombolites. Such microbialite structures are observed both in pure carbonate settings and mixed carbonate-siliciclastic environments. Thus, there was sufficient space between the sea floor and the undersides of coral colonies for the development of crusts 5–8 cm thick. These observations suggest a definitely low accumulation rate during periods of microbialite growth. Thrombolitic columns with upward growth are present both in pure carbonate settings and in mixed carbonate-siliciclastic environments. They also formed the upper part of mammilated microbialites of the bioherm flanks or of pseudostalactitic microbialites. Olivier et al. (2003) have demonstrated that the different microbialite morphostructures tend to show an upward growth direction, suggesting probable positive phototropism of the microbial structures in coral-microbialite reefs. Chafetz and Buczynski (1992) noted that lithification takes place several millimetres below the water/biofilm interface, where heterotrophic bacteria degrade organic matter. Considering a complex composition of microbial mats, including cyanobacteria, bacteria, and extrapolymeric substances (EPS; van Gemerden 1993; Stolz 2000), even though fast growing photoautotrophic cyanobacteria are not responsible for carbonate precipitation, they probably controlled the direction of microbialite growth. On the other hand, light-control of microbialite growth is indicated by some lamellar corals with thrombolitic columns only on their upper surface, whereas thicker and massive microbialitic crust is observed at their underside. Though available space was certainly limited, lower illumination levels between the coral underside and the sea floor could be responsible for reduced microbial development, which resulted in the formation of only a thin crust of massive microbialite.

Reef development and controlling factors

Reef growth phases

During coral-microbialite reef formation, large biogenic skeletons (e.g. corals and bivalves) were the primary frame-builders (Scoffin and Garret 1974) that furnished the substratum for the diverse encrusting sequences forming the secondary framework (Bosence 1984). The primary frame-builders and the first encrusting organisms generally are photophilic forms. As the bioconstruction developed, and with beginning of overgrowth, many of the secondary and shade-loving frame encrusters were restricted to cavities within the reef (Brenchley and Harper 1998). Nevertheless, this purely autogenic evolution of the reef structure can be largely complicated by the interference of allogenic factors such as terrestrial runoff (e.g. Hallock et al. 1988; Dupraz and Strasser 2002). Encrusting sequences have been used in several Upper Jurassic coral-microbialite reefs to reconstruct the variation in time of several environmental parameters such as illumination, trophic conditions and oxygenation (Helm and Schülke 1998; Dupraz 1999; Dupraz and Strasser 1999, 2002). In the bioherms of the different reef-building events studied in the Pagny section, the following general succession of reef communities or reef growth phases have been found (Fig. 15):

1. Installation and growth of the macrofauna consisting mainly of corals and cemented bivalves that form the primary framework (stage 1). This primary framework is eventually covered by a first generation of encrusters including *Bacinella irregularis*, *Lithocodium aggregatum*, and *Solenopora jurassica* Brown (stage 1')
2. A second encrusting layer made by a millimetric crust of dense micrite associated with numerous nubeculariids, *Tubiphytes*, some bryozoans, and a few calcareous sponges (stage 2)
3. A centimetric thrombolitic crust either peloidal or dense to clotted with *Terebella lapilloides* (stage 3).

Reef growth: an autogenic or allogenic growth process?

The reef communities of each reef-building event described show significant adaptations both in their composition and in the succession of their encrusting organisms. In a pure carbonate setting (RE1), the primary framework (i.e. coral assemblage) and the first generation of encrusters (*Bacinella*, *Lithocodium*, and *Solenopora*) are interpreted as indicators of nutrient-poor and well-illuminated waters. In mixed carbonate-siliciclastic environments, the lack of the first photophilic generation of encrusters and the mixotrophic coral assemblages suggest more turbid waters and/or a higher nutrient level. Considering the primary frame-builders and the first generation of encrusters, abiotic factors such as light and terrestrial run-off seem to have directly controlled the composition of framebuilders. Thus, allogenic (i.e. extrinsic) factors are dominant during reef growth stages 1 and 1' (Fig. 15).

Reef growth stages 2 and 3 are essentially similar, both in pure carbonate settings and in mixed carbonate-siliciclastic environments. Nubeculariids, bryozoans, and calcareous sponges, associated with a thin crust of dense micrite (i.e. reef growth stage 2; Fig. 15) could encrust dead coral surfaces in slightly less illuminated zones within the reefs (Dupraz 1999; Dupraz and Strasser 1999, 2002). Reef growth stage 3 showing a large amount of clotted to peloidal micrite could be explained by the prevalence of nutrient-rich and oxygen-depleted interstitial waters within the reef framework (Sansone et al. 1988; Tribble et al. 1990; Haberstroh and Sansone 1999), favouring microbialite formation (Sprachta et al. 2001). Due to a new generation of coral overgrowth, intrareef environments became less illuminated and thus favourable for the installation of sciaphilic organisms such as *Terebella* and *Bullopora*. As a consequence, the reef growth stages 2 and 3 observed in all of the coral-microbialite reef-building events (RE1, RE3, RE4, and RE5), could be interpreted as being autogenic (i.e. dependant of intrinsic factors). However, a purely autogenic control in the formation of extensive microbialites several centimetres thick, observed on the flanks of the coral-microbialite reefs (i.e. reef growth stage 3; Fig. 15), is not sufficient. Such external microbialitic development implies a shift to environmental conditions favourable for a microbially mediated carbonate precipitation, both within the reef and in its surroundings. Thus, the large microbialitic development observed during reef growth stage 3 was due to external factors that probably predominated over possible autogenic factors—i.e. light and oxygen decrease and nutrient-rich waters within the reef—in controlling the physico–chemical conditions prevailing within and around the bioconstructions (Fig. 15).

In pure carbonate and mixed carbonate-siliciclastic settings, coral-microbialite reefs developed either during periods favourable for coral growth or during periods more propitious for a microbialitic development. If purely autogenic processes are sufficient to explain a part of reef growth (i.e. reef growth stage 2), allogenic factors are directly responsible for phases of intense microbial growth and abundant $CaCO_3$ precipitation (i.e. reef growth stage 3; Fig. 15). This is the case both within the reef body and at its periphery, and thus detrimental to coral growth (Reitner 1993; Camoin et al. 1999).

Climatic control

Sea-level variations show a low-frequency regressive trend in pure carbonate environments and a transgressive trend in mixed carbonate-siliciclastic settings (Fig. 4). However, sedimentary features indicate that bathymetric changes were relatively small (a few metres) during development of the different coral-microbialite reefs. Thus, bathymetry cannot be the only factor responsible for the differences in reef composition during different reef-building events, and for the successive growth phases observed in the reefs. Main changes in coral assemblages, in primary and secondary encrusters, are presumably controlled by variations in the nutrient level that was in tune with climatic conditions (Fig. 14).

Dry climate probably coincided with pure carbonate deposits (Gygi 1986; Gygi and Persoz 1986; Pittet 1996; Pittet and Strasser 1998; Vincent 2001) leading to growth of photophilic and oligotrophic organisms (*Aplosmilia* - stylinids and *Lithocodium* - *Bacinella*). Under such oligotrophic conditions, coral assemblages tended to develop over a large area and formed pluridecimetric bioconstructions. These extensive reefs thrived under conditions of generally moderate water energy interrupted by brief events of very high energy.

The presence of large truncation planes in RE1 reefs suggests that such catastrophic storm or hurricane events occurred in fact. In recent reefs, these disturbances resulted in extensive surfaces of dead corals (Woodley et al. 1981; Hughes 1994). After such events, a high concentration of nutrients present in pore waters could be released during resuspension of organic matter buried in lagoon sediments (Sarazin et al. 1988; Gagan et al. 1990; Russ and McCook 1999). The richness in organic matter combined with coral mortality favoured rapid benthic blooms of algae, since algae grow and colonise much faster than corals (McCook 2001). The reef system of Jamaica at Discovery Bay shows a recent example of such an algal bloom that occurred after a major hurricane disturbance (Hughes 1993, 1994). Algal predominance and the failure of coral communities to recover persisted over more than 20 years, probably enhanced by overfishing and anthropogenic eutrophication (Lapointe 1997; McCook 1999). However, after algal cover reached a critical point, algae could prevent or limit coral recovery and settling by coral larvae. This would explain an algal predominance of several years (McCook et al. 2001; McCook 2001). Furthermore, some cyanobacteria have the ability to produce chemical defences that may deter herbivores, facilitating cyanobacterial blooms in coral reef habitats (Nagle and Paul 1998). Other examples of modern algal blooms are reported from the Buck and Virgin Islands reefs, where algal blooms were observed after Hurricane Hugo in 1989 (Rogers 1993).

Microbialite formation induced by temporal pulses of nutrient release has already been mentioned for Quaternary coral-thrombolite reefs (Camoin et al. 1999; Sprachta et al. 2001). Considering a very low thrombolitic growth rate of 1 mm/year (Thompson et al. 1990; Schmid et al. 2001; Leinfelder 2001), a 50-year period would be sufficient for the formation of a 5 cm thick microbialitic crust as observed locally in a RE1 reef. Assuming a probable fast growth of microbial mats, it is quite possible that such a crust required only a few years to develop. Progressively, eutrophication vanished and conditions of normal, oligotrophic marine water progressively returned. This allowed settlement of new coral larvae and enhanced carbonate production (Hallock and Schlager 1986). As a result of higher accumulation rates, knobby, low- or non-encrusted outer surfaces of thrombolites that had developed during the nutrient-rich periods in RE1 reefs, were rapidly covered. Thus, oligotrophic conditions that prevailed during the RE1 reef-building event resulted in an important reef expansion, only interrupted by brief periods favourable for cyanobacterial blooms and rapid microbialite deposition.

Stronger rainfall causing increased terrigeneous input led to a mixed carbonate-siliciclastic regime, as observed in the upper part of the section (Figs. 4 and 14). Under these mixed depositional conditions, minor sea-level fluctuations would induce changes in the trophic conditions, which in turn could affect reef ecosystems by closing or opening shallow lagoons (Pittet 1996; Pittet and Strasser 1998; Dupraz 1999). Periods of closure of the lagoon and high terrigeneous input resulted in argillaceous deposits with only small oyster reefs (RE2). On the other hand, coral-microbialite reefs (RE3, RE4, and RE5) that developed laterally into bioclastic and/or oncolitic limestones (facies 2 and 3) are characterised by a reduced or moderate siliciclastic input and moderate to high water energy (Figs. 14 and 15). In such environments, minor changes in terrigeneous input and/or trophic conditions enhanced either mixotrophic or heterotrophic coral assemblages, or formation of microbialites (Dupraz and Strasser 1999, 2002). The bioconstructions appear relatively small in size, probably because of the high participation of microbialites that did not have the same capability as corals to enlarge the bioconstructions. Periods of reduced terrestrial run-off and waters of low turbidity are indicated by the prevalence of more balanced heterotrophic/phototrophic corals and bivalves (Fig. 14).

Contemporaneously, only a thin microbialitic crust associated with heterotrophic organisms (nubeculariids and bryozoans), and calcareous sponges lived just below the reef surface. In these shallow lagoons, periods of higher sediment run-off led to increased trophic levels (and alkalinity?) of waters, enhancing the formations of extensive microbialites (Neuweiler et al. 1996; Camoin et al. 1999; Sprachta et al. 2001). Under these conditions, the coral framework was finally covered by microbialites (Dupraz 1999). Periods of high terrigeneous input increased the turbidity in the water column and resulted in a high sedimentation rate that could directly affect the benthos. However, turbidity does not necessarily result in high accumulation rates (Woolfe and Larcombe 1998; Larcombe et al. 2001). It allows a large development of microbialites such as those observed in RE5 reefs. On the other hand, too turbid waters tend to diminish light intensity with the possible disruption of growth of light-dependent microbialites. Thus, successive periods with illumination levels too low for cyanobacterial development probably controlled the formation of microbialites with several interruptions of the growth phase. On the other hand, this reduced development of biofilms and microbial mats allowed an important oyster settlement and an intense activity of reef boring organisms, enhanced by a higher nutrient level (Hallock 1988). Thin (up to 1 cm thick) massive microbialitic layers that underline microbial growth interruptions can be compared with the basal crusts described by Schmid (1996) and with the crusts covering hardgrounds as observed by Reitner et al. (2000). Compared with pure carbonate settings, coral-microbialite reefs occurring in these mixed carbonate-siliciclastic environments are notable for a reduced reef growth, which is detrimental to a more intense and longer microbialitic development. In some cases, shifts towards major terrigeneous input and/or increased trophic conditions led to interruption of growth of the bioconstruction.

Conclusion

The Pagny-sur-Meuse section provides an excellent example of how reef ecosystems react in response to an environmental shift from a pure carbonate to mixed carbonate-siliciclastic sedimentation. Five successive reef-building events document the changes in the coral fauna, as well as the development of microbialites and associated micro-encrusters that occurred in these different palaeoenvironments.

1. Slight sea-level oscillations could explain recurrent facies changes between marl deposits and bioclastic carbonate facies in mixed carbonate-siliciclastic settings. However, these variations in water depth cannot be responsible for the drastic facies change that occurred between the depositional environments of pure carbonates in the lower part of the section and the mixed carbonate-siliciclastic sediments in the upper part. Sedimentological changes were probably triggered by terrestrial run-off in response to a rise in humidity due to climate change as was previously recognized by studies of shallow lagoon deposits in the Swiss Jura along the northern margin of the Tethys.
2. The sizes of the coral-microbialite reefs and of frame-building coral colonies appear negatively correlated with the influx of siliciclastics. Pure carbonate sedimentation appears favourable for extensive reef development, whereas mixed carbonate-siliciclastic settings favour the formation of small patch reefs. Only small metric oyster reefs are observed in marly deposits that are devoid of corals.
3. A high diversity coral fauna, consisting mainly of phaceloid forms such as *Aplosmilia* and *Stylosmilia* predominated during pure carbonate sedimentation under oligotrophic conditions. Terrigeneous input and increase of the nutrient level prevailing in reefs of

mixed carbonate-siliciclastic settings are accompanied by a balanced heterotrophic/phototrophic to heterotrophically dominated nutritional mode of the coral fauna. The diversity and abundance of the stylinids decrease, whereas the mixotrophic massive, lamellar and encrusting forms of moderate size (e.g. *Microsolena*) dominated the coral assemblages. When wave energy levels increased temporarily or locally in nutrient-rich settings, diversity became considerably reduced and the sturdiest corals such as *Calamophylliopsis* and *Thecosmilia*, associated with *Microsolena* predominate the coral fauna. A large amount of cemented bivalves also indicates mesotrophic conditions. In too muddy environments rich in siliciclastics, oysters and various encrusters (serpulids and bryozoans) exclusively formed the bioconstructions in which corals were absent. Thus, the different coral assemblages observed at the Pagny-sur-Meuse section appear mainly to have been controlled by variations in the trophic conditions.

4. Microbialites are most abundant in mixed carbonate-siliciclastic settings, but they are astonishingly well-developed also in pure carbonate settings. However, they are rare in argillaceous environments. Both in mixed carbonate-siliciclastic and pure carbonate environments the secondary framework shows two main microbialitic crusts. The first crust corresponds to a thin and dense micrite associated with heterotrophic encrusters such as nubeculariids, bryozoans, and calcareous sponges. We believe that this crust was formed during almost the same environmental conditions as coral growth, probably in slightly less illuminated zones on dead coral skeletons just below the reef surface. It thus appears to be autogenically controlled. The last and pluricentimetric stage of microbialitic growth is documented by peloidal or clotted micrite that seems to have been controlled by allogenic factors. Peloidal micrite is generally observed in thrombolitic columns, whereas dense and clotted micrites are abundantly overgrown by diverse encrusters, suggesting a more continuous and faster growth for peloidal micrite.
5. Different microbialite morphostructures in coral-microbialite reefs show a direction of microbialitic growth that tends to become vertical, suggesting probable positive phototropism of the microbial structures. Growth interruptions of microbialites probably resulted from both too nutrient-rich and too turbid waters, which allowed an abundant encrusting fauna to install and an intense bioerosion.
6. Periods of extensive microbialite development are interpreted as diachronic with periods favourable for coral growth and seem to have been directly triggered by regional abiotic factors that led to an increase in nutrients (and alkalinity?). Two different scenarios may explain extensive microbialite development: (1) an increase of terrigeneous input in mixed carbonate-siliciclastic environments and/or (2) catastrophic storm events that redistribute sediments and nutrients in the reef environment of pure carbonate settings.

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